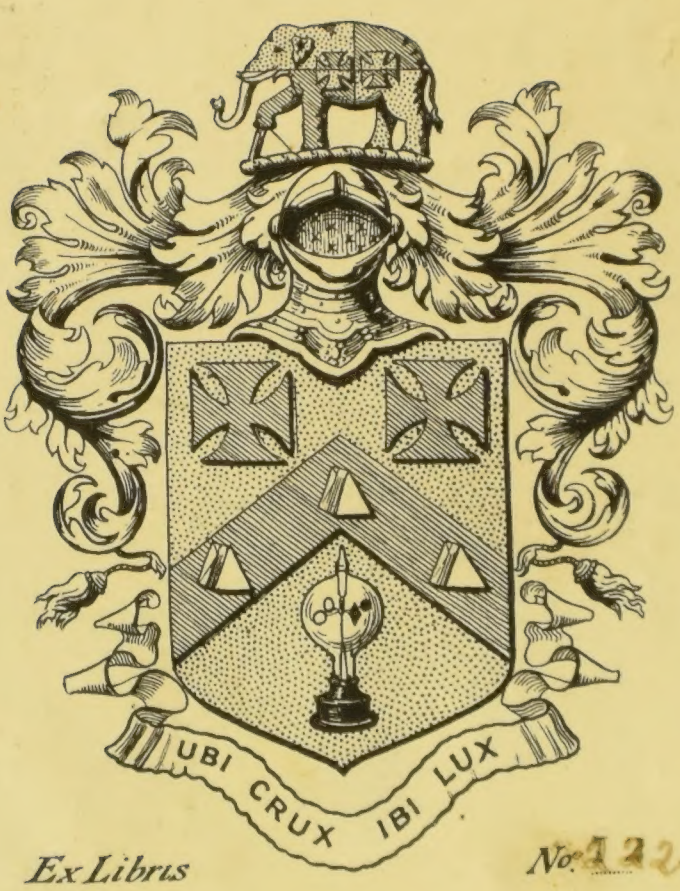
EUGENIO RIGNANO

UPON THE INHERITANCE OF ACQUIRED CHARACTERS



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INHERITANCE OF ACQUIRED CHARACTERS

Eugenio Rignano

UPON THE

Inheritance of Acquired Characters

A HYPOTHESIS OF HEREDITY, DEVELOPMENT, AND ASSIMILATION

AUTHORIZED ENGLISH TRANSLATION

BY

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WITH AN APPENDIX

UPON THE MNEMONIC ORIGIN AND NATURE OF THE AFFECTIVE OR NATURAL TENDENCIES

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"Some deny flatly the possibility of ever arriving at an understanding of the nature of life. But if we ask ourselves in what this understanding of the nature of life could consist, from the point of view of positive philosophy, we have no difficulty in recognizing that such an understanding must be reduced to comparing vital phenomena with some physico-chemical model already known, suitably modified by the particular special conditions imposed upon it so that just these special conditions shall determine the differences which exist between this vital phenomenon and that phenomenon of the inorganic world most closely related to it. If this be so, it is then the duty of science emphatically to refuse to give up the attempt to understand the nature of living matter, for that would be to belie the Spirit of all scientific endeavor. For whether it be clearly recognized or not, it is just this search for the nature of the vital principle which properly constitutes the principal object and the final goal of all biologic study in general."—E. Rignano, in "Acquired Characters," p. 334.

TRANSLATOR'S PREFACE

Rignano is a student of Biology who has also the training of an engineer and physicist. His attack on biological problems is from that side. In this book he offers an explanation on a physical basis of assimilation, cell division, and the biogenetic law of recapitulation in ontogeny, and he suggests a mechanism whereby the inheritance of acquired characters may be effected.

Such a study of the most fundamental and difficult of biological problems can not fail to be of the greatest interest to all students of science. It points out a way to the understanding of the essential nature of living matter. Therefore the translator has gladly consented to prepare for publication this translation first made for his own satisfaction. It has been revised by the author.

University of Chicago, 1911.

BASIL HARVEY.

PREFACE TO THE ENGLISH EDITION

This work which appeared first in French in 1906 and later in German and Italian now appears after some years in English thanks to the interest shown by several English and American biologists and philosophers, who have expressed a desire to have its circulation facilitated among the savants of their countries. This new indication of the growing favor acquired in a short time by the theories here advanced, notwithstanding the author's fear that their novelty would stand somewhat in the way of their reception, is the best reward he could desire for the great difficulty he has encountered in the study of these—the most fundamental problems of biology. And he wishes to pay here his sad and affectionate respect to the revered memory of Professor C. O. Whitman, one of the first to interest himself in this English edition, and at the same time to express his gratitude to his friend Dr. Basil Harvey for the great care which he has given to the translation, as well as to Dr. Paul Carus and The Open Court Publishing Co., who have been so good as to become the publishers.

Milan, March, 1911. E. R.

INTRODUCTION

The question of the inheritance of acquired characters is one which, by its generality, by its importance for the theory of the origin of species, and by its close connection with still more difficult questions concerning the essential nature of life lying in the border land between physical chemistry and biology, passes beyond the confines of pure biology, and enters the wider field of positive philosophy in the sense of August Comte, that is of scientific philosophy, which concerns itself with the most general results of the various sciences and with their fundamental interrelations. Is it any wonder then that this much discussed but unsolved question excites the keenest interest in philosophers and even induces some of them though they are not specialists, to attempt to study it thoroughly utilizing the abundant and valuable material which biologists and naturalists can now supply?

It is so with the author of the present study.

Formerly when he had not yet formed any fixed and definite opinion upon this subject, he had been inclined in a few philosophical and sociological studies to prefer Weismann's theory of the non-inheritance of acquired characters to the contrary theory of Lamarck. The reason for this inclination even though no logically tenable opinion had been formed, lay in the demonstrated inability of any of the biological theories which had then been

devised to give any explanation whatever, even an unsatisfactory one, of the mechanism of that inheritance. Yet the author never lost sight of the fact that natural selection in no way sufficed to explain phylogenetic evolution completely, and he was always convinced that non-inheritance was irreconcilable with the fundamental biogenetic law that ontogeny is only a recapitulation of phylogeny. This law, whose remote and immediate consequences constantly stimulated the reflection of the author, has finally led him in a purely inductive way to the new biogenetic hypothesis about to be presented.

It seemed to the author that he ought to devote a special effort to the elaboration and exposition of this hypothesis, for he saw from the outset that it promised an explanation not only for the inheritance of acquired characters but also, and quite independently, for a whole series of fundamental biological phenomena, and how it afforded an outlet from the blind alley into which ontogenetic biology seems to have run: for while some facts lead us to reject epigenesis as it is commonly understood, others force us to reject preformation, and similarly while a whole series of reasons force us to hold as inadmissable a homogeneous germinal substance or a substance only chemically heterogeneous, another whole series of reasons obliges us to hold no less inadmissable a germinal substance constituted by the germs of the preformists.

The author knows well that he must not entertain any oversanguine expectations. In the position of biological science today we can deal only with preliminary hypotheses, of which each gives way to its successor and each, taking in a greater number of phenomena than its predecessor prepares the way for a later hypothesis which

is able in its turn to include a number greater still. So soon as a hypothesis pushes a bit nearer to the beleaguered fortress, so to speak, and indicates new lines for study, observation and research, one must admit that it has fulfilled its purpose. And this applies to our view of the new biogenetic hypothesis which we here submit to the judgment of biologists and of positive philosophers in general.

We have believed it expedient to follow in the exposition of this theory the order in which it was conceived and built up, and so the first chapter describes briefly the inductive way in which the author, starting out from the fundamental biogenetic law, was led to the conception of his hypothesis. In the three following chapters are collected and arranged as concisely as possible the principal, different, biogenetic facts which, quite independently of the ever controverted question of the inheritance of acquired characters, serve best to set forth and define the new hypothesis and which, since they find in it their most complete explanation, confirm it again directly or indirectly in a deductive way.

After having then undertaken in the fifth chapter a brief examination of the question of the inheritance or the non-inheritance of acquired characters which until then we had laid entirely aside, we pass in the sixth chapter to the critical exposition of the principal biogenetic theories which are current at present. And we do this not only with the object of showing their inadequacy to explain the mechanism of inheritance, but rather in order that the perception of the reason of this inadequacy may aid us in discovering the necessary and sufficient conditions required in any theory which seeks to explain this inheritance. After that we go on again in the seventh chapter with the examination of our hypothesis whose

conception and elaboration up till then was considered quite independently of the question of the possibility or impossibility of the inheritance of acquired characters, but which supported by an elementary hypothetical phenomenon, which in certain respects finds its counterpart in the inorganic world, becomes recognizable at once as a most complete explanation of this inheritance.

Finally in the last chapter we endeavor to show how this elementary hypothetical phenomenon on which the new biogenetic theory rests, explains also a fundamental, psychic phenomenon, to wit, memory and indeed the most characteristic properties of the vital phenomenon in general. And so this elementary hypothetical phenomenon seems to us capable of bringing together within it and referring to one basis not only the whole group of genetic phenomena, but all vital phenomena whatever in the very widest sense of the word.

Since, for the reasons above stated, the inheritance of acquired characters is a question affecting positive philosophy in the Comtian sense or scientific philosophy, the author ventures to hope that biologists and naturalists may not regard him as an unbidden intruder into their domain, but rather since he is the first to recognize the many gaps and shortcomings of his work, he ventures to hope that he may count upon especial consideration, because of the great difficulties with which he who is no specialist has had to contend in studies of so difficult a nature.

Milan, May, 1905. E. R.

ONTOGENY

CHAPTER ONE

ONTOGENY, AS A RECAPITULATION OF PHYLOGENY, SUGGESTS THE IDEA OF A CONTINUOUS ACTION EXERTED BY THE GERM SUBSTANCE UPON THE SOMA THROUGHOUT THE WHOLE OF DEVELOPMENT.

Everyone knows the fundamental biogenetic law of Haeckel: ontogeny is a recapitulation of phylogeny, that is, the development of the individual is a rapid résumé of the development of the species, a short reproduction of the endless chain of its ancestors.

The most important facts establishing this law, now perhaps irrefutably, are so well known that we hardly need to mention them here; for example: solipedation develops gradually in the horse and only in the last stages of its development; many whales which later instead of teeth have the so called whalebone have teeth in their jaws while they are still in a fetal condition and cannot take any nourishment; the serpent while it is in the embryonic state possesses its two pair of limbs, and so on.

"The development of the organism," writes Roux, "is not merely a production of the complex from the simple by the most direct route. The ways are devious; and many a forward step must be retraced. We mention only the well known examples of the gill clefts and gill arteries and their ultimate concrescence, the notochord also, and the pituitary and pineal glands, structures quite super-

fluous and functionless from the first." [1] Development of this sort, proceeding toward its goal not by the direct line but by byways and often backwards, would be incomprehensible were it not for the fundamental biogenetic law.

Also Delage draws attention to the fact that all those structures which disappear during the progress of development must nevertheless have their significance.[2]

Similarly Oscar Hertwig notes expressly that there exist many embryonal organs "which never come into a position to perform the function which they have once performed during the course of phylogeny." [3]

We must then regard this fundamental biogenetic law as true. We can even suppose it to be a close approximation, that ontogeny represents phylogeny exactly.

It is true that during the first ontogenetic stages phylogeny is only epitomized, but this becomes steadily less true the farther development proceeds, and during the later stages ontogeny can be regarded as an almost exact repetition of all the corresponding phylogenetic stages.

The human embryo, on account of the more numerous and careful researches of which it has been the object, serves better than any other to illustrate this almost exact phylogenetic repetition in the later stages. Its development demonstrates even to the smallest details how the embryo passes through the whole series of forms of the pithecanthropoids, its immediate ancestors. Thus for example the articulations of the leg in man show during

[1] Wilhelm Roux: Der Kampf der Teile im Organismus. Leipzig, Engelmann, 1881. P. 59.

[2] Delage: L'hérédité et les grands problèmes de la biologie générale. Paris, Schleicher, 1903. P. 176.

[3] Oscar Hertwig: Die Zelle und die Gewebe. Zweites Buch. Jena, Fischer, 1898. P. 232.

fetal life a much closer resemblance to those of anthropoids than during adult life. At a certain stage of development the great toe instead of being parallel to the others forms an angle with their direction as in the apes. In the same way many of the bones of the foot of the newborn infant, in their form, in their respective angles of inclination, etc., resemble very closely those of the climbing foot of the anthropoid apes, particularly of the gorilla.

In the attempt to see what significance the fundamental biogenetic law can have for the biologist we can come somewhat nearer to the question by supposing ontogeny to be an exact repetition of phylogeny instead of a rapid résumé of it. It is true that it will be necessary later to make some important corrections in this first approximation and to study the significance or cause of the abbreviation and suppression in ontogeny of many phylogenetic stages; and this more intimate study will allow us to penetrate further into the innermost nature of the phenomenon. But for the present we desire by this tentative supposition that ontogeny is an exact repetition of phylogeny, to have the great advantage of defining the phenomenon to be studied more simply and precisely, and of making our comprehension of it correspondingly easier. It is by this means, that is by successive degrees of gradual approximation that mechanical, physical, and chemical researches have usually proceeded.

This first degree of approximation of the fundamental biogenetic law will permit us then to make the two following statements: Each stage of the ontogenetic development of any organism represents exactly one species among the ancestors of that organism. Two species having a common ancestor have an identical ontogenetic

development up to the stage corresponding to that common ancestor; they do not commence to diverge until they have passed that stage.

But since all the various theories of heredity admit that two distinct species descending from a common remote ancestor possess germinal substances different from each other, the question at once presents itself: If these germinal substances are different, how then is it possible that throughout a long series of stages up to the stage corresponding to the common ancestor they present like ontogenetic forms, the very same as those through which the ancestor passed? If the germinal substance of one species is different from that of the other should they not from the very beginning show a totally unlike series of forms?

A germinal substance in process of development constitutes to a certain extent a dynamic system of forces in continual transformation. But two systems commencing to give rise to two series of successive transformations which throughout a long time are quite alike must necessarily be themselves alike. And if at a given moment one series diverges from the other it is necessary to attribute this divergence to one of two causes; either to some external circumstance acting at that moment, or to some internal impulse becoming active just at that moment.

"The parallelism in the phenomena of ontogeny and phylogeny," says Delage, "shows that first something develops which is similar to what was developed in the ancestors, and that then something which remained till then inactive is added and development proceeds further." [4]

[4]Delage: L'hérédité etc., P. 457.

In other words the biogenetic law implies that up to each stage of development the productive cause of development remains the same as that which produced the ancestral species corresponding to that stage.

We should next ascertain whether the new circumstance now added or the new force becoming active only at this stage and causing the subsequent development is to be sought for within or without the various parts of the organism which are actually in process of formation.

If at the start we limit ourselves for the sake of simplicity to the consideration of morphological transformations only, each stage of development whether ontogenetic or phylogenetic will appear to us only as a special mode of distribution of the organic substance constituting the organism. But this distribution is modified during the life of the adult individual only by new functional stimuli, that is to say, only by agents which are external to the structure in progress of modification. In other words the impulse by which the corresponding portion of living organic substance is constrained to distribute itself differently does not reside within this portion but comes to it from without.

Until the contrary is proven we may accept the statement that the properties of living organic substance during development are not different essentially from those which it presents when development is completed. Consequently when any particular mode of distribution of the organic substance becomes altered during the progress from one given ontogenetic stage to the succeeding stage, we can admit as a provisional hypothesis that this different distribution is effected by some provocation external to the parts which change.

This provocation cannot be constituted merely by the

morphological and physiological state of the other part of the organism at that moment; for in the corresponding phylogenetic state the two portions were in perfect equilibrium with each other. It is necessary then to suppose that somewhere in the remaining parts of the organism, there enters into play just at that moment and only at that moment, some factor which was not present in the ancestral species.

Further, since the alteration in the organism during ontogeny is not confined to a single part of the organism but affects several parts at the same time, and since the impulse which comes into play at the end of each stage of development compelling the passage to the successive stage must lie external to each of the parts undergoing transformation, it cannot lie in any of these parts.

This will be possible, however, only on condition that among all the different parts of the organism there is at least one part which is not itself subject to any substantial change, but in which there comes into activity a series of specific energies one after another of which each provokes the passage of all the other parts of the organism to the next ontogenetic stage.

This special part may be called the central zone of development. And one can give the name of centro-epigenesis to this hypothesis by which ontogenetic development is made to depend on an infinite number of different influences which this zone gradually exerts upon all the remainder of the organism by activating successively a regular series of specific energies, each remaining in a potential state up to the time of its activation.

Now the part which actually does remain unaltered from the first segmentation of the egg up to the giving off of the reproductive cells by the new organism is the

germinal substance, and one suspects at once that it may be just this substance which constitutes the central zone.

If so it would follow that the central zone must be at the same time the germinative zone, that is to say, the place whence the sexual cells get the germinal substance which makes them capable of reproduction. Let us hasten to add now that the central zone must coincide with the effective germinal zone, but may possibly be quite separate and distinct from the apparent germinal zone. The latter would be then only the place of formation of the sexual cells, inasmuch as these constitute in a certain sense the mere envelope in which later the germinal substance is assembled, which alone is able to give them reproductive capacity.

The hypothesis of centroepigenesis includes then that of a continuous action exercised by the germinal substance upon the soma throughout the whole duration of its development. We shall endeavor in the second chapter to learn what is the nature of this action and we shall reserve for consideration in the third chapter the central zone itself, as well as other facts and arguments which make its existence seem probable and which serve to make the hypothesis clearer.

We shall limit ourselves here to putting in special light the fundamental characteristics which differentiate this hypothesis as well from the preformistic as from the epigenetic theories.

While Weismann and the preformists in general consider that the germ plasm separates itself before the commencement of development from the portion set apart to form the new organism, and remains passively aside in a detached part of the soma until it later steps in to form the future sexual cells; consequently it would not control

development nor indeed have any part whatever in it; that would fall entirely to the other portion alone, and it would be just this passivity which would secure the inalterability of the germ plasm:

While on the other hand the epigenesists consider that the idioplasm would participate in an important and continuous way in development, because it would be present and active at every instant and in all cells; it would remain, however, in spite of this participation permanently unaltered, so that the cells of the soma would never become differentiated by nuclear somatization from the germ cells, but on the contrary retain the capacity of reproduction to the same extent:

The centroepigenetic hypothesis postulates on the contrary that the germinal substance, although limited to a single zone and separated and differentiated from the rest of the soma, nevertheless exercises its epigenetic, formative action upon all the rest of the organism and during the whole of development, without undergoing any alteration whatever through this participation in development.

But this hypothesis thus sketched must now be made more precise and clear by the consideration of other series of phenomena, while at the same time the proof of the facts is undertaken. And to this we propose to proceed in the chapters which follow.

CHAPTER TWO

PHENOMENA WHICH INDICATE A CONTINUOUS FORMATIVE ACTION WHICH IS EXERTED BY PARTS OF THE SOMA UPON THE OTHER PARTS THROUGHOUT THE WHOLE OF DEVELOPMENT—HYPOTHESIS OF THE NATURE OF THE FORMATIVE ACTION.

1. *Phenomena Which Indicate a Continued Formative Action*

Among the phenomena which seem to indicate indisputably a continuous formative action exercised by a more or less great part of the soma upon the other parts throughout the whole of development, those of the regeneration of amputated organs take a first place.

It is known that when the antennae of a snail, the chelae of a crab, the feet of a salamander or the head of a worm are amputated, these organs are reproduced even when the amputation is performed during adult life.

Spallanzani has cut the feet and tail off the same salamander six successive times, and Bonnett seven times, and each time feet were reproduced of exactly the same size as the former ones without any increase or decrease in any part. These facts show that the formative agent whatever it may be is always external to the part formed, and that it exercises upon the whole development of that part and throughout its entire duration a continuous action, and further that it remains itself unaltered even

after the completion of its work and consequently is capable of renewing it at every favorable opportunity.

If on account of unusual conditions the regeneration of the amputated part proceeds in an abnormal fashion, the remaining part continues always in spite of that to be capable of normal regeneration. For example: an axolotl had a foot bitten off. The foot was reproduced but badly formed. This foot was amputated and a third was developed which was quite normal.[5]

We shall later at a proper place treat of the ill-starred attempts of the preformists to bring their theory into accord with similar phenomena, and of the arguments and the special regenerative processes which the epigenesists have brought forward in support of their theory. Here it may merely be noted that while epigenetic theories furnish an immediate explanation for all phenomena of regeneration, the preformation theory on the contrary must have recourse to the addition of complicated subsidiary hypotheses which are entirely opposed to the principal one.

If the morphological capacity does not reside in the somatic cells of the cut surface, which by their multiplication produce the regenerated organ, but is outside these, it follows that the continuous action exercised upon all cells at the end of the regenerated part as also upon all cells which do not lie at the cut surface, by the remaining part of the organism must be a mediate action exercised from a distance, and therefore must traverse intermediate cells.

A yet more striking demonstration of a continued,

[5]Darwin: The variation of animals and plants under domestication. Eighth impression of the second edition. London, Murray. 1899. P. 357, 358.

formative action exercised mediately and at a distance by one part of the organism upon another during the entire development of this latter is furnished by the famous experiments of Roux in the post-generation of his half embryos.

The words in which he describes the process of this post-generation which he has observed in half embryos obtained from frogs' eggs after he had killed one of the first two blastomeres with a hot needle, deserve to be reproduced here in full.

But we must remember at the outset that while the uninjured blastomere develops into only a half embryo, the injured blastomere lying beside its neighbor produces often a late fragmentation of its protoplasmic mass consisting only of undifferentiated cells. And this is effected in one of the following two ways, either through only partial killing of the nucleus concerned some individual fragments of it continuing to live and multiply, or through an emigration of naked nuclei from the part of the egg remaining intact into the protoplasm of the injured blastomere. Now we quote Roux.

"Postgeneration of germ layers of half organisms proceeds always from the already differentiated germ layers of the normally developed half of the egg. It extends thence first to the yolk mass subsequently cellulized, especially where such a germinal layer is in contact with such a mass by a broken surface and consequently by the lateral surfaces of its cells."

"The formation commencing at this point proceeds steadily and continuously through the yolk mass of the undeveloped half of the egg. About the free margin of the advancing germinal differentiation there are to be found gradual transition stages between the undiffer-

entiated yolk cells and the cells of the already completely differentiated germinal layer. With the elimination of other possibilities this leads us to the conclusion that the progressive differentiation is accomplished in material already in position before differentiation commenced, and remaining there throughout it, and therefore in passive yolk material by direct transformation of the yolk cells (accompanied in the case of the ectoderm and mesoderm also by the division of these cells)."

"As to the location of the causes of these processes," continues Roux, "we can draw a few further conclusions."

"Since the yolk cell material later differentiated to form the germ layers in the manner described above has been quite disordered in its substance forming the bodies of the cells, by the operation, and since also the nuclear material of the cells which are later formed from it has never yet taken its place by virtue of a typical division, but, being derived partly from the nucleus of the half operated upon and partly from the emigrated naked nuclei of the half remaining intact, owes its disposition to the chance of the moment, therefore the conception, possible in the case of normal development that at typical places there is always deposited typical material capable of quite definite independent development, cannot be admitted in this case."

"We must conclude rather, that the cause of this typical formation of the germ layers of the first developed half of the egg, extending into the half operated upon, lies in forces which proceed from the germ layers of the first half."

"I conclude, then, that in our postgeneration the progressive differentiation extends in space as the result of a direct assimilating and differentiating action exercised

by differentiated cells upon other less differentiated cells which are immediately adjacent to them."

"In the latter process very different degrees of action are possible. There can, for example, emanate from the differentiated cells an influence which simply sets free the process of differentiation allowing the entire series of necessary changes after this preliminary impulse to proceed of itself. Or, each of these changes may not merely receive from the differentiated cell a simple initial impulse, but may on the contrary be determined by that throughout. Between these two extremes one can imagine a whole series of intermediate stages. On account of the at first atypical disposition of the material which at last becomes typically differentiated I am inclined to think that the action of the differentiated cells upon the nondifferentiated cells is not a mere liberating one or a mere stimulating one." [6]

These facts of postgeneration indicate then above all that the action of the half embryo already formed upon the other half in process of formation is exercised in a continuous manner throughout the whole development of this latter.

One would be led also to this conclusion, that there is a continuous action exercised throughout the whole of development, by the fact that the postgeneration of the undeveloped half goes on with greater rapidity, so that it soon overtakes the other half and proceeds with it to the same stage of development.

[6] Wilhelm Roux: Uber die künstliche Hervorbringung „halber" Embryonen durch Zerstörung einer der beiden ersten Furchungszellen, sowie über die Nachentwicklung, Postgeneration der fehlenden Körperhälfte. Virchows Archiv, Bd. 114. October 1888, P. 279—282. Gesamm. Abhandl., Zw. Band. P. 507—509.

This continued action leads us to conclude also that as a further consequence a remote action is exercised by the half embryo already formed upon the parts of the other half which are not in direct contact with the first. This remote action can be transmitted only through all the intermediate cell layers which lie between the surface of contact of the two half embryos and the remote parts in process of postgeneration.

It would seem necessary then to conclude that the first half embryo exercises upon the far removed parts of the second a remote, mediate and continuous action.

We shall now provisionally assume that postgeneration does not differ in its essential nature from direct generation, and note some consequences which follow for the hypothesis of the central zone of development which during normal ontogenesis would exert an action similar to that which the half of the embryo already formed exerts upon the other half during postgeneration.

The nuclei obtained as the result of the first divisions of the egg and destined to become somatic, even though derived from those which according to this hypothesis would later form the central zone, would then have to be considered, in relation to the somatizing stimulus exerted by that zone, as quite like the indifferent nuclei of the embryonal half capable of post generation, which receive now this now that stimulus without any preference from the half already developed, and become somatized in consequence now in one way now in another way according as they may chance to be disposed.

The indifference in respect to somatizing stimuli of these nuclei, which we should at least at the outset suppose like those nuclei from which they are derived, and which later according to this hypothesis give rise

to the effective germinal zone, leads us to a second hypothesis, namely: that the especially germinative energies of those nuclei destined to become somatic may be once for all silenced, that is once for all put in a potential state incapable of activation, on account of the preponderance which the nuclei that go to form the effective germinal zone or central zone acquire.

In fact we can suppose that the first blastomeric nuclei, though exactly alike qualitatively, are different quantitatively, that is to say are furnished with amounts of energy which do not chance to be quite the same in all, perhaps on account of special conditions of nutrition or, perhaps, on account of special conditions of the protoplasm in which they are placed. Then, as soon as the moment comes when because of the nature of the commencing transformation, such as perhaps invagination or some such thing, embryonal development can no longer proceed after the same fashion in all cells, certain ones will necessarily gain the upper hand, namely those which possess more potential energy.

The other blastomeres whose nuclei would no longer be able to activate their germinal energies will from now on conduct themselves, in relation to the stimuli of the nuclei of those blastomeres which constitute the central zone of development, just like cells with indifferent nuclei. And with the progressive somatization of these latter the mass of their respective specific elements to which is due the persistence, potentially at least, of their germinal energies, will gradually diminish and finally disappear.

There is only a single conceivable exception, namely the case in which at the beginning of development or in inferior forms, these blastomeres or cells just beginning

to be somatized accidentally remain isolated, in which case the activation of their potential germinal energies would be permitted, which might have been impossible had they remained united with the other blastomeres or cells.

The possiblity of such receptive indifference toward somatizing stimuli in nuclei which if they were isolated or in other conditions would on the contrary possess and give practical demonstration of very definite specific qualities, is indicated by those cases in which all the nuclear material of the post generated half embryo is furnished by the half already developed.

Indeed it often happens that on the side operated upon the nutritive yolk alone is utilized; and into this latter emigrate nuclei formed by normal division of the nuclei of already somatized cells in the developed half of the egg. And these emigrated nuclei then bring about the division of the yolk mass of the part operated upon into small indifferent cells only: "With the formation of a right or left half embryo," Roux observes in a later study, "the formative capacity of the uninjured half of the egg is not yet exhausted. On the contrary certain experimental results permit the conclusion that in many cases there is an emigration from it of nuclei, and perhaps indeed, of a little protoplasm also, going out from those points which by the accident of position have the most intimate contact with the side operated upon, toward the contiguous half of the egg deprived of its own capacity of development. These nuclei become distributed throughout the whole of the large mass of yolk and thereupon follows later a breaking up of the half operated upon into cells, and this is not as in normal division a division of the whole mass first into two nearly

equal and consequently large cells, which divide again later in their turn each into two correspondingly smaller cells and so on; but on the contrary the breaking up is from the first into small cells."

It is upon these indifferent cells that the half of the egg already developed exercises its formative action. These nuclei which arise from cells of the half of the embryo already developed must nevertheless possess very definite specific properties; some come from ectodermic cells, others from mesodermic and others from entodermic cells. And if the medullary plate, the notochord, etc., have already been formed, the vagrant nuclei come also from cells which are in an advanced stage of development. And yet when they have once emigrated and have become scattered through the yolk of the injured side, they remain no less indifferent in relation to the formative stimuli which come off later from the part already formed, than in the cases where they arise entirely from the injured half of the egg. From whatever cells of the embryonal half already developed they may have been produced, they are capable of any somatization whatever, for this depends only on the place at which they happen to stop or become arrested during their migration into the yolk plasma of the injured half of the egg.

The same thing can take place in the blastomeric nuclei also as soon as they once find themselves outside the group, which, according to the hypothesis above stated, would form the central zone of development: in relation to the ontogenetic stimuli which from now on

[7]Wilhelm Roux: Uber das entwicklungsmechanische Vermögen jeder der beiden ersten Furchungszellen des Eies. Verhandlungen der anat. Ges. Wien. June 1892. P. 34, 35. Gesamm. Abhandl. Zw. Bd. P. 782, 783.

are sent out from this zone, they conduct themselves in a quite indifferent way, though for a greater or less time they preserve their germinative capacity potentially.

While the experiments of Roux carried on carefully and with astonishing exactness of observation, demonstrate directly the continued remote and mediate action which the formative part exercises upon the part being formed throughout the whole of development, the existence of this action is confirmed by other investigations, in a way which though indirect is not any less certain on that account.

They comprise all the cases in which the part removed is regenerated by cells histologically different from those of normal generation, for instance in which organs or tissues of ectodermic, mesodermic, or entodermic origin are reproduced in the regeneration by tissues having a different blastodermic origin.

It will suffice for our object to recall the most typical example which has stirred up the two hostile camps of the epigenesists and the preformists; we refer to that of the regeneration of the lens in the eye of the tritons, which, after its extirpation, is reproduced from the cells of the iris, that is to say, from a material quite different in character from that of which it is formed in normal generation.[8]

The double epithelial layer of the iris, from the marginal proliferation of which the new lens springs, must exercise upon the lens in process of formation a continuous action persisting throughout the development

[8]See e. g. Erik Müller: Uber die Regeneration der Augenlinse nach Exstirpation derselben beim Triton. Archiv f. mikrosk. Anat. und Entwicklungsgesch. Band, XLVII. erstes Heft. Bonn. Cohen, 1896. P. 23 ff., especially 29 and 30.

of the lens. For the cells of the iris cannot preserve within them potentially any trace of a formative capacity, or of a germinal "anlage," or of any "determinant" which provokes the formation of the lens, seeing that in normal development the latter takes its origin from another tissue.

In these examples, both in the post generation of Roux's half embryos and in the regeneration of the lens in the triton, the cells which serve as constructive material appear then to be absolutely incapable of any auto-transformation and ready on the contrary to differentiate themselves and to dispose themselves indifferently in any manner whatever, according to the formative stimulus to which they happen to be exposed.

At this point the fundamental biological question presents itself: What is the nature of these formative stimuli, of this continued action which the formative part exercises upon the part being formed?

The attempt to build up a hypothesis relating to so important a question is the object of the studies presented in the second part of this chapter.

2. *Hypothesis of the Nature of the Formative Stimulus*

If, in our study of the nature of the formative stimulus in the development of organisms, we start with the primitive pluricellular form, consisting simply of aggregations of cells that are all alike, we observe that during some stages of their ontogeny the essential nature and the behaviour of these cells is clearly determined by phenomena of nervous nature in the widest sense of the word. For example, phenomena of this nature exist undoubtedly in the little mononuclear amoebae into which the spores of the myxomycetes become changed, also in

the zoospores which move about by means of their vibratile flagella and into which these mononuclear amoebae become transformed. And it is certain that phenomena likewise nervous in character must come into play when the cells of Magosphera planula become separated from one another and each one moves off independently by means of its cilia.

One is justified then in suspecting that when these cells are united in a colony they may then also be the seat of phenomena of a nervous nature, and that the other ontogenetic stages of these minute organisms ought also to be attributed to such phenomena.

But then we should have to refer the development of higher organisms also to phenomena of the same nature.

As a support of this hypothesis we recall the well known fact that all cells of organisms, from these most primitive pluricellular forms up, are united to one another by a network of intercellular protoplasmic bridges.

We recall the example which the different species of Volvox afford, a genus of lower algae consisting of a vesicle formed of a single layer of cells, very much like the blastula stage of the development of animals. All the species of Volvox show a perfectly typical and regular form of union between the different cells of the body. In Volvox aureus for example, the superficial cells of the trophic hemisphere of the vesicle lie in a thick soft gelatinous mucus and each is not only provided with two long flagellae, but also is connected with each of the five or six adjoining cells by a long, thin protoplasmic filament. In the germinal hemisphere the protoplasmic filaments are more numerous so that each of the great spores which arise there is connected with each one of the large neighboring cells by bundles of from three to

six filaments. These protoplasmic connections persist for some time even when the spores have been divided into two, four, or more constituent parts.[9]

An experiment which has already become famous appears to indicate that the intercellular bridges, as if they were successors of the vibratile protoplasmic filaments, substituted for them, are traversed incessantly by nervous currents or discharges emanating from the nucleus. For this experiment we are indebted to Pfeffer.

After having detached by plasmolysis the cell membrane of the nucleated protoplasmic body of a plant cell, and dividing the cell into halves, one containing a nucleus and one without any, he observed that only the nucleated half had surrounded itself with a new cell membrane. If however, the part deprived of the nucleus remained united to the nucleated fragment even by only a very fine protoplasmic filament, it also was capable of secreting its little cellulose membrane.

Pfeffer varied his experiment also in the following manner. He prepared cells of a moss protonema in such a way that an entirely isolated, anucleate mass of protoplasm remained united to the neighboring cell which contained a nucleus by means of thin filaments piercing the cell wall. In this case a membrane was formed round the anucleate fragment. But the membrane was not formed if the neighboring cell had been itself deprived of its nucleus.

In the formation of this cellular membrane in anucleated parts of the cytoplasm united by protoplasmic filaments with other nucleated portions, the maximum intervening distance observed by Pfeffer was 3.7 mm.

[9]Oscar Hertwig: Die Zelle und die Gewebe. Zw. Buch, P. 34, 35. Fig. 16, 17.

"But the nucleus can certainly exercise the membrane forming stimulus at an even greater distance." If the nucleus remains united with a whole chain of anucleated bits of cytoplasm "the production of the membrane appears to advance centrifugally and so to commence a little later in the more remote portions of cytoplasm, than in the bits nearer the nucleus." [10]

From these experiments one is inclined to think, this author concludes, "that the production of a cellular membrane required the continuous transmission and cooperation of certain states of motion and vibration which radiate out from cell nuclei or rather owe their origin to the reciprocal action of nucleus and cytoplasm."

Oscar Hertwig makes in this connection the following remark: "This experiment proves that the stimulus necessary for membrane formation can be transmitted by thin connecting filaments which traverse the septum interposed between two cells. Nothing hinders us then from assuming that some similar transmission goes on in other functional conditions." [11]

In these observations of Pfeffer the formation of the membrane goes on independently of the situation and remoteness of the nucleus and of the geometric form of the line of communication which may be straight or curved in any way, and consequently, (and we must keep this especially in mind,) just as though this formation were effected by a specifically stimulating current, passing

[10]Pfeffer: Uber den Einfluβ des Zellkerns auf die Bildung der Zellhaut. Berichte über die Verhandl. der königl. sächs. Gesellsch. d. Wissensch. zu Leipzig. 1897. P. 507.

[11]Oscar Hertwig: Die Zelle und die Gewebe. Zw. Buch, P. 40, 41.

out from the nucleus and quite independent of the form and extent of the conductor which carries it.

But it is very probable that this nervous current or discharge which is conducted from the nucleated cell along the protoplasmic filaments to the anucleated fragment of the contiguous cell, also passes across into the fragment even when it contains a nucleus and so also when it is replaced by an entire cell. This leads us to the conception that wherever intercellular protoplasmic connections are present, the various nuclear currents or discharges stream through these connections and so permit a general nervous flux throughout the whole network of these protoplasmic bridges, in the meshes of which the nuclei themselves would constitute the nodal points. In this way one would have a continuous circulation or distribution of nervous energy throughout the entire organism.

This supposition is supported by the experiments of Siegfried Garten. On his own arm he cut out a little disc of skin one centimeter in diameter so as to lay bare the muscle fibers. Without suturing the wound he covered it with an aseptic dressing and left it to the process of granulation. After the wound was completely covered with epithelium except only a small circle of 1.75 mm. radius he cut out the whole piece again and enough around it to reach to the area in which the skin was in quite normal condition.

Microscopic observation gave the following result: Studying it from the center of the wound out, one met first of all a greater or less number of wedge shaped epithelial cells with the long axes radially disposed. Surrounding this came next an annular zone, 0.45 mm. broad, of fusiform epithelial cells whose long axes were

almost without exception tangentially disposed, that is perpendicularly to the radius of the wound, and the protoplasmic filaments within the cells ran parallel with their axes. In correspondence with this interior cellular arrangement, the intercellular bridges into which the protoplasmic filaments were prolonged ran for the most part from tip to tip of the fusiform cells and parallel to their long axes.

Outside this annular zone, (from 2 to 2.5 mm. outside the inner epithelial border,) were found large cells in which the filaments and protoplasmic bridges were remarkably well developed and there also were found mitoses. It is therefore in this area that new cells are formed. In this zone the intercellular spaces are larger than elsewhere, from 3 to 6 μ wide, whereas 1.8 to 3 μ represents the mean normal figure for the epidermis. This considerable enlargement of the intercellular spaces makes it possible for these cells to store up the larger quantity of nutritive fluid which is necessary for their more intense activity.[12]

If one admits for the moment that the intercellular bridges are traversed by a continuous nervous flux this result will find in this hypothesis its immediate explanation.

In order to make our idea clearer let us consider the concrete case of a stream of flowing water, which at a certain point divides up into several branches. Sooner or later a dynamic equilibrium is established and the quantity of water flowing during each unit of time into each of the branches respectively will be constant. If

[12]Siegfried Garten: Die Interzellularbrücken der Epithelien und ihre Funktion. Archiv für Anatomie und Physiologie. Leipzig. 1895. P. 407—409.

we now effect artificially the obstruction of some of these branches the entire volume of water must flow through the others which remain open and their volume of water will consequently be increased in proportion.

In the same way let us suppose that through the intercellular bridges of the epidermis for example, there go similar nervous currents, in which when once the organism has attained its adult age dynamic equilibrium is established. And let us remove a little disc of skin as Siegfried Garten did, then the nervous flux which heretofore had taken its way through the filaments and protoplasmic bridges of the cells situated in the little disc removed will now find these ways closed. Consequently the entire flux must take a roundabout way through the neighboring parts surrounding the little disc.

The augmentation of the nervous current in these ways will have as its result an augmentation of the trophic stimulus which it exercises; so that the cells situated along these ways will grow and proliferate more rapidly, thus producing a zone of reproduction characterized by numerous mitoses. The augmentation of the vital processes of these cells will in consequence of increased osmotic attraction, attract a greater quantity of nutritive fluid, exactly as the wick of a lamp which is stimulated by a current of air draws up by capillarity a larger quantity of combustible fluid. And this greater quantity of nutritive fluid pressing in between one cell and another, will distend the intercellular spaces so that in this zone they undergo an enlargement. The further the new formation of the skin proceeds, the shorter will be the way through which the abnormally increased nervous flux tends to pass, that is to say that the zone of the

most intense flux and the zone of reproduction thereby determined will approach the center of the wound.

The tangential disposition of the cells of the circular zone between the reproductive zone and the central granular zone, would be due just to this nervous flux which commences to flow through the new formed cells, but is still always forced to flow around the wound in some such way as the water of a river flows around the circular pier of a bridge. The direction of the cell axis would thus be determined by the direction of the current.

According to Siegfried Garten's views, on the contrary, there would exist all around the wound, in spite of the aseptic dressing, an augmentation of the blood circulation, which would have as its consequence an increase of pressure and of the amount of nutritive fluid in the tissue. And consequently there would arise an augmentation of volume of the intercellular spaces and an increased formation of new cells in the reproductive zone. As for the tangential disposition of the cells of the surrounding zone, he believes that one can explain that by the theory of sphincter action, that is through the contraction of the intercellular bridges of these cells. In consequence of this contraction the long axis of the cells would turn into the direction of the tractile force which is exercised upon the cells. At the same time the consequent shortening of the respective circular zones of these cells would cause the epithelium to press in toward the center of the granulating surface, and thereby effect the gradual contraction of the opening of the wound.[13]

But the increased blood supply and the shortening

[13]Siegfried Garten: Ibid. P. 409—411.

of the intercellular bridges which this explanation presupposes would require to be explained themselves. It is to be remembered further that Roux in his studies upon the struggle of the parts of the organism has shown that the great affluence of necessary nutritive fluids is always the consequence rather than the cause of the growth of the organic substance.

This experiment of Siegfried Garten argues strongly in favor then of the hypothesis that a continuous nervous flux traverses the intercellular bridges. The nuclei, as foci of nervous energy, would be precisely the sources which feed it, and which in normal conditions preserve it unaltered. At the same time, the nervous flux discharged by the other nuclei in passing through any one nucleus acts like a functional trophic stimulus, in so far as it is favorable to the specific vital process of this nucleus. Each increase or decrease of this current passing through certain nuclei caused by conditions lying without these nuclei, would have as a result an augmentation or diminution first of their mass and later of their number.

This augmentation of the nervous flux in given zones following the ablation of neighboring parts would thus be the general cause of the active proliferation of cells by which all the phenomena of reproduction commence.

Later when there comes into play a disturbance of the equilibrium, one can conceive that its reestablishment can proceed and spread from any one whatever of the numerous parts which surround the part cut off. In other and more general terms one understands that the reestablishment of the normal distribution of nervous energy, necessary for the reformation of an organ, in case it be prevented from following the ordinary way,

can reach the organ by any other way and indeed by a way quite the opposite of the normal as happens for example in any distribution of electric or hydrodynamic energy, and that consequently it amounts to the same thing whether the regeneration of the tissue or of the organ ablated proceeds in the same way as in ontogeny or by any other way.

And finally we must suppose that regeneration is nothing else than a particular case of generation or reproduction and that the nature of one is substantially identical with that of the other: for, to use the words of Delage "generation is only the regeneration of a complete organism by a portion of greater or less size attached to it or detached from it;" [14] so the causes of the regeneration, for instance of a little disc of skin which has been removed, must be essentially the same as those which effect a complete reproduction.

Between the two phenomena the following difference will however exist: The regeneration of a little disc of skin will be due, according to what we have just stated, to the fact that the continuous nervous flux which flows through the whole organism and particularly through those parts which were contiguous with the part removed, would tend to reestablish its dynamic equilibrium, disturbed by the operation. If we accept the fundamental biogenetic law in its first degree of approximation, complete generation, on the contrary, would be a whole series of transitions of the nervous energy circulating or distributed in the developing organism, from one dynamic system to the other next in order, both meanwhile being in a state of equilibrium since they were already formerly

[14] Delage: L'hérédité et les grands problèmes de la biologie générale. P. 98.

in equilibrium in both the corresponding phylogenetic forms. To effect the transition it is necessary then that in each ontogenetic stage there suddenly supervene at some point of the system a change, which disturbs the established equilibrium and provokes the passage of the continuous nervous flux to a new dynamic equilibrium.

If the intercellular bridges have really the significance which we have attributed to them, one can see how they must be present in all organisms and in all stages of development. It is superfluous to go more thoroughly here into the fact that this is exactly what is fully confirmed by histologic investigations which are being ever more carefully prosecuted.

We recall for example the protoplasmic connection observed by Hammar between the segmentation spheres of the sea urchin egg: The cells of the blastula are covered all over the outside of it by a protoplasmic layer which adheres in each cell only to the part of its surface which is directed toward the outside. This layer in a few preparations not sufficiently protected against drying separated itself a little from the blastula. There appeared then thin filaments, variable in number and more or less regular in disposition, which extended from the granular protoplasm of the different blastomeres to the interior of this layer and produced in this way a manifold connection of the different cells with one another.[15]

Sedgewick has observed the same thing in the development of the eggs of Peripatus. The two cells which come from the cleavage of the eggs are not completely

[15]Hammar: Ubereinen primären Zusammenhang zwischen den Furchungszellen des Seeigeleies. Archiv für mikrosk. Anat. und Entwicklungsgesch. Bd. XLVII. Erstes Heft. Bonn, Cohen. 1896. P. 14ff.

separated but remain connected by protoplasmic filaments; the cells which arise from each of the first two cells are associated in the same manner, and this continues indefinitely. So that during the whole of development from the first segmentation of the egg up to the adult stage all the cells of the organism remain in intercommunication by means of these protoplasmic bridges. "The connection of cell with cell is not a secondary feature acquired late in development, but is primary dating from the very beginning of development." [16]

It is quite unnecessary to recall the universality of intercellular bridges not only between the cells of each tissue but also between the cells of different tissues: between the epithelial cells of gland ducts and contiguous smooth muscle cells, between epithelial cells and connective tissue cells, between connective tissue cells and endothelial cells, between smooth muscle cells and connective tissue cells, between connective tissue cells and striated muscle fibers, between striated muscle fibers and epithelial cells, and so on.[17]

It is necessary to be remarked further that in animals this circulation of nervous currents can and at least in certain stages of development must certainly utilize not only the protoplasmic network uniting the cells to

[16]Adam Sedgwick: The Development of the Cape Species of Peripatus. Quart. Journ. of microscopical Science. XXVI, 1886. P. 198—200, 206.

[17]See for instance: Heidenhain: Uber das Vorkommen von Interzellularbrücken zwischen glatten Muskelzellen und Epithelzellen des äusseren Keimblattes und deren theoretische Bedeutung. Anat. Anzeiger, VIII, No. 12 and 13; May 13, 1893; P. 404—410; and Schuberg: Uber den Zusammenhang verschiedener Gewebezellen im tierischen Organismus. From the Sitzungsberichten der Phys.-Med. Gesellschaft zu Würzburg. Sitzung vom Febr. 25, 1893; P. 1—8.

one another, but also the nervous system itself with all its fibers and fibrils in so far as it is developed. This leads to the conclusion that in the adult organism the ordinary nervous currents passing along the various nerves as a result of ordinary nervous discharges constitute only momentary intensifications of permanent nervous currents which pass continually through these nerves.

The great frequency with which conductors of nuclear stimuli in general and intercellular bridges in particular, are found in both animal and vegetable kingdoms, is as we have said, even by itself a very strong support for the hypothesis proposed by us of a nervous circulation or distribution throughout the whole organism.

In this hypothesis we approach, even though only in certain respects, the most recent theories of some botanists and physiologists who in consideration of this striking general protoplasmic connection between the different cells, regard the multicellular organism not as a mere assembly or colony of cells, but rather as a single voluminous protoplasmic body in which the nuclei are inserted at different intervals as centers or foci of energy, (synergids of Sachs), and in which the membranes and other intermediate structures have produced only incomplete divisions and serve merely as supports of the organism. For example, according to Sedgewick the body of the adult animal would be only an immense syncytium whose nuclei or centers of force are dispersed throughout a single protoplasmic network binding together the whole organism.[18]

We approach especially the conception which Oscar

[18]Adam Sedgwick: The Development of the Cape Species of Peripatus. P. 205—206.

Hertwig seems to have of protoplasmic connections, for while it is true that he never discusses such a continuous nervous flux and speaks only of the transmission of nuclear stimuli, nevertheless this latter conception in our mind implies the former. To sum up our conception of these protoplasmic connections we could almost adopt the very words of this investigator: "It is probable that this transmission of nuclear stimuli by protoplasmic filaments will be much less rapid and less intensive than nerve conduction, but perhaps for this very reason will be more continuous and by reason of its duration more efficacious." [19]

It is quite unnecessary to draw especial attention to the fact that the vegetable kingdom is not in any way an obstacle to this conception of a continuous nervous flux throughout the whole organism, for if nervous phenomena are less apparent in it than in the animal kingdom, they constitute nevertheless just as in the latter the essence of the vital phenomenon.

From amoeboid movements, from the vibrations of cilia and flagella up to the most complex psychic phenomena, everywhere where life is, one finds also processes of nervous nature. The reticular or fibrillar structure which protoplasm in general exhibits, protoplasmic currents, especially those in very long, fine filaments, such as for example those in the pseudopodia of the rhizipod Gromia oviformis, which by their peculiar character make one suspect that they may be only the consequence and sensible effect of currents provoked by an energy of another kind, the striations consisting of bundles of curved parallel lines without sharp angles in

[19]Oscar Hertwig: Die Zelle und die Gewebe. Zw. Buch. P. 40.

each little layer of the cell membranes of plants, the formation of a membrane in an anuclear fragment of a vegetable cell in consequence of a nuclear stimulus transmitted from the nucleus of another cell along any protoplasmic conductor, all these facts speak together in favor of the hypothesis that all living substance is traversed by vital nervous energy in the form of currents.

Claude Bernard has already remarked that anaesthetics act not only upon the nervous system but also upon the cells of every animal or vegetable tissue, in that they destroy or suspend the vital activity of every cell in the same way, and from that he concludes that all vital processes in general are substantially identical.[20]

This substantial identity is demonstrated further by the fact that phenomena of irrito-contractility present themselves in the same way in both animal and vegetable kingdoms and that there are all possible transition stages between plants considered "especially sensitive" and those considered not sensitive at all. The whole group of "especially sensitive" plants present especially well developed intercellular protoplasmic connections.[21]

We recall further the microscopic movements of the protoplasm within the membranes of plant cells, which led Huxley to make the well known definition that a plant is only "an animal shut up in a wooden box."

Everybody knows that in addition to these microscopic movements there are now known in plants also various movements visible to the naked eye, which cor-

[20]Claude Bernard: Leçons sur les phénomènes de la vie communs aux animaux et aux végétaux. Paris, Baillière, 1878. P. 289—290.

[21]Macfarlane: Irrito-contractility in plants. Biol. Lect. at the Mar. Biol. Lab. of Wood's Holl. Summer Session 1893. Boston, U. S. A., Ginn. 1894. P. 189, 204.

respond fully with the reflex movements of animals; that is, in which one can distinguish as in animals a region of perception and another of motility, as well as the transmission of a stimulus from the perceptive region to the motor region.

Leaving aside the very well known example of Mimosa it suffices to recall for example, that in certain plants one can demonstrate that the sensibility of the root to gravitation resides in its extreme tip while the bending movements of that same root in order to resume its vertical position after it has been disturbed takes place in another part. In the same way the vertical position of the stem is maintained. But a yet more typical example is furnished by the grass, Setaria. "It has a remarkable manner of germination; as soon as the seed germinates it does not produce a simple cylindrical stem but one terminating in a wedge shaped tip like a lance head. When a group of Setaria is lighted from one side it inclines strongly toward that side and all the lance tips point toward the light. But these tips are not curved at all, on the contrary the whole bending is produced in the stem, although it is clearly these tips which are sensitive to light and not the stems. It is easy to prove this by covering the tops of some stems with an opaque cap: the grass stalks so protected remain vertical while others incline their stems toward the light. The part that bends has not then any sensitiveness to light and the part sensitive to light does not bend. The little lance is the organ of perception, the stem the motile region, and it is clear that a stimulus is transmitted from the tip to the stem." [22]

[22]Francis Darwin: Le mouvement chez les plantes. Revue scientifique. March 1, 1902. P. 265.

Consequently the view is not only justified but almost required that in plant bodies also there is a nervous circulation or distribution, which, though it manifests itself only in its variations dependent on some change in the external influences, is certainly none the less present during the repose of the organism when it is in a state of dynamic equilibrium. It is this constant circulation or continuous distribution of nervous energy, which constitutes in plants quite as well as in animals the "small yet mighty link" which unites the parts of the organism into a "sympathetic whole," a function which Lewes ascribes especially to the nervous system.[23]

As to the properties of each of the respective excitatations or currents which constitute this general nervous flux, it is sufficient for our purpose to suppose that these latter appear in specifically differing modes of existence which are capable now of combining now of disjoining; we mean by this that two specific modes of being are able for example to combine with each other and so to give rise to a third specific mode of being, or indeed that this latter can break up giving rise to the two preceding specific modes of being or even to others different from them.

While for the present we are not in a position to discover what these different specific modes of being really are, yet we can and indeed must necessarily regard them as existing since in different tissues different specific nuclear stimuli must certainly be present in the cells. These different specific modes of being might consist in something analogous with the intensity of the continuous electric current, or perhaps in a rhythmic form correspond-

[23]Lewes: The physical basis of mind. New edition. London, Kegan Paul, Trench, Trübner & Co. 1893. P. 61.

ing somewhat for example with the alternating electric current, or indeed might arise in another way of which perhaps we can not in advance form any conception at all. It is sufficient for our purpose, we repeat, to suppose that these specific modes of being can combine and break up according to laws which are definite even though so far quite unknown. For the very fact of the existence of these laws would imply also the existence of corresponding laws on which the circulation or distribution of nervous energy in definite networks would depend.

If one accepts such a hypothesis of the circulation or the distribution of nervous energy in the organism, one could find the immediate explanation of certain phenomena of development whose cause has so far remained a secret. These phenomena consist in the reciprocal influences which certain parts of the embryo, even though widely separated, exert upon one another in spite of the lack of any functional adaptation and by which the development of these parts is wholly or partially determined.

One can, indeed, attempt to give the beginning of an explanation of these phenomena of correlation, by supposing the different parts which exercise this reciprocal influence to be situated, maybe upon the same partial network of the general circulatory system, maybe upon different partial networks which nevertheless come off at one common given point from the same principal branch, or maybe finally, in the case of contiguous parts, upon different partial networks which are however provided with direct communications between some of their respective nuclei. The absence of any analogous reciprocal action between other parts also contiguous may be explained by the lack of any such direct con-

nection between the nuclei of the two partial networks belonging to these parts, a fact which renders these networks in certain respects quite independent of one another if at the same time they do not come from a common principal branch.

It would be "a very important matter," writes Delage "to know if secondary protoplasmic connections are formed between neighboring cells which are not sisters but which have been brought only secondarily into contact with one another, for example after an invagination in animals or through grafting in plants." [24] In the cases in which this did not occur one could then have the simultaneous and to a certain extent independent existence of partial circulatory systems even though they lie close together or perhaps even enclose each other.

Roux designates by the term "correlative or dependent differentiation" the complete or partial determination of development by reciprocal influences of epigenetic nature which become established, in a certain measure at least as he admits himself, between the cells. We can then designate these partial networks of the general circulatory system by the name "networks of correlation." And we shall see that, conformably with our theoretical conjectures very many processes seem actually to prove that each of these networks is capable of existence by itself, independent within certain limits of other partial networks.

Among the phenomena of correlative differentiation in development belong also those which are called compensatory growths. The investigations of Ribbert (1889) and his pupils upon the mammals have shown especially

[24] Delage: L'hérédité et les grands problèmes de la biologie générale. P. 33.

well, that after the cutting off of organs not yet in function, for example of the testicle or of an infantile ovary or several infantile milk glands, the other similar organs underwent in their respective parts a proportionate growth as though they would thus compensate for absent parts. It would appear from this that the networks of correlation belonging to each of these parts of like organs must come off from a common principal branch in such a way that the whole current of this branch prevented from the usual division by the absence of one part of the network would now discharge itself entirely into the remaining organ.

The hypothesis of the continuous circulation or the continuous general distribution of nervous energy which thus finds its support in certain special phenomena of development, affords better than any other an explanation for the fundamental process of every ontogeny, which consists as Roux has very aptly said only in a series of unequal localizations of growth.

"A given region grows," writes Delage, "while the neighboring parts by which it is surrounded, grow much less or not at all. This part must necessarily then project outward or become invaginated and form a cavity. But at a given moment growth ceases in this place and goes over to another place, and the same phenomenon is now repeated at this new place." [25]

The morphological means which ontogeny employs is then always the same, always of the same identical nature even when the tissues already partially differentiated commence to differ from one another in their most essential properties.

[25]Delage: L'hérédité et les grands problèmes de la biologie générale. P. 174.

The hypothesis of a continuous trophic nervous flux being admitted, these serial unequal localizations of growth can be explained by changes in the distribution of this flux at each new ontogenetic stage, from causes which we shall examine in the next chapter. These changes of distribution bring about now here, now there, a great affluence of nervous energy and thereby induce at the corresponding points proliferation of the cells from which must necessarily arise later the invagination or evagination in question.

But the ontogenetic phenomena which most clearly call for the conception of such a distribution of nervous energy which continually changes and shifts, streaming now through one region now another of the developing organism, are the phenomena of involution; that is to say phenomena of reduction presented by the tissues of an organ which after being formed in the course of ontogeny tends at a later stage to disappear; for example the involution of the tail of a tadpole during its metamorphosis into a frog.

The atrophy and degeneration of the skin, of the notocord, of nerve and muscle fibers, by which this involution is produced, have been described particularly by Osborn. He as well as Metschnikoff has established in this connection the great phagocytic activity of certain cells and the formation of true and false giant cells. Nevertheless he does not attribute to the phagocytes the most important role in the elimination of material. The whole of the process, in fact, results in the gathering together of the cellular material in process of disintegration and conducting it into the lymph and blood vessels for utilization later in the construction of other organs and tissues peculiar to the adult animal.

This would indicate then that the greater phagocytic activity would be not so much the cause as rather the effect of the diminution of the vital resistance of the organ. And this latter would seem necessarily to be due exclusively to the fact that the organ itself would be at this ontogenetic stage abandoned by the particular energy which had formed it, and which up till now had maintained it in full vital activity, and which now has not indeed ceased to exist, but has turned to other regions. This transference of cellular material in process of disintegration to other organs and tissues in process of formation would seem in fact to demonstrate that simultaneously with the diminution or the cessation of the trophic stimulus in one given region there appears an increase of that stimulus in another region.

This utilization, as nutritive material, of the substance of cells which are disintegrating is rendered necessary by the fact that animals during their metamorphosis take almost no nourishment. It follows that, if the nutritive material which the abandoned parts give up to the parts now more abundantly infused with trophic energy, should be insufficient at the normal rapidity of disintegration, the disappearance of the tissues must be accelerated. This is indicated by Osborn's researches upon the influence of fasting upon metamorphosis, from which it appears that it is appreciably accelerated by inanition, just because of the more rapid reduction and absorption of the organs about to disappear.[26]

In the disappearance of the tail of the tadpole one has not a senile but rather a premature involution of tissues,

[26]Osborn: Alte und neue Probleme der Phylogenese. Ergebn. d. Anat. u. Entwicklungsgesch., herausg. v. Merkel u. Bonnet. Bd. III. 1893. Wiesbaden, Bergmann. 1894. P. 198.

"in which nature destroys in a manner which may seem to us cruel, cells which have just been produced." The hypothesis of the distribution of trophic nervous energy seems to us the only one which can give a satisfactory explanation of this phenomenon.

The struggle of the parts of the organism cannot in fact be the exclusive cause of this involution of young tissues. This struggle is not sufficient by itself to explain the exactness of the epoch and of the stage of development at which this physiological involution takes place. Even if we were willing to admit that this struggle has some effective participation in the production of this phenomenon, we must nevertheless admit that in addition an inciting ontogenetic stimulus, as Roux would say, must at the appointed time exert its trophic action upon the parts destined to victory, while it abandons others previously favored, but which now are devoted to destruction. The distribution of trophic nervous energy with its changes would thus always remain the only cause of the phenomenon.

But if ontogenetic physiological involutions are due to the fact that the distribution of trophic nervous energy abandons one region to turn to another, similar changes and shifting of this distribution must then be likewise the cause of all invaginations and evaginations, of all morphological phenomena in general and, with much probability, consequently, of those ontogenetic phenomena also which are not exclusively morphological in nature.

To produce each one of these serial ontogenetic modifications in the distribution of trophic nervous energy it would suffice theoretically that at the required moment there become active, were it only upon one certain point of the circulatory system, a single new definite specific

current, different from the current previously present at the same point. And this would be exactly the role, which as we have already said the central zone of development plays. This zone therefore will be the object of our study in the next chapter.

CHAPTER THREE

PHENOMENA WHICH POINT TO THE EXISTENCE OF A CENTRAL ZONE OF DEVELOPMENT—HYPOTHESIS OF THE STRUCTURE OF THE GERMINAL SUBSTANCE.

1. *Phenomena Which Point to the Existence of a Central Zone of Development*

The only group of organisms in which one can say that the existence of a central zone of development is directly demonstrated is that of the unicellular organisms, in which this zone is constituted by the nucleus. In pluricellular organisms it is only indirectly that we are able to arrive at the conclusion that the central zone exists.

Experiment has shown that the necessary and sufficient condition for the ontogenetic development of the Infusoria is the presence of a nucleus. This latter constitutes therefore for them an effective central zone of development and consequently ontogenesis consists in them in a true and proper centroepigenesis.

If one divides an amoeba or a rhizopod or an infusorian already completely developed, into many pieces, that one of these fragments which remains provided with its nucleus though it be the smallest of all, is yet capable of reproducing by new formation all the missing organs and of developing again into a normal individual; whereas the

other fragments, without nuclei, are incapable of it even though they may be much larger.

Especially we recall the researches upon artificial division of the Infusoria made by Nussbaum and Gruber. If, for example, one cuts a stentor into three pieces, of which each contains one portion of its moniliform nucleus, in the space of twenty-four hours each piece regenerates the missing part. The anterior extremity regenerates the posterior and vice versa; the middle piece reforms the two extremities, that is to say, both the rather complex peristomal region with its mouth, its pharynx, its long cilia, etc., and also the simpler posterior part. If however the fragment retains no part either of the paranucleus or of the nucleus proper, even though it may be of much greater size than those fragments retaining the nuclei, no trace of regeneration is observed, a fact which does not prevent the piece concerned from continuing to live for a while, even for two or three days, nor from retaining completely the capacity of locomotion, of vibration of cilia, of pulsation of the contractile vesicle, of defecation, of capturing, engulfing and digesting its food.[27]

Gruber reports however the following experiment which has caused a good deal of surprise, for according to the view of some biologists it seems to be opposed to the results of earlier researches.

He selected a Stentor coerelus which showed already the first stages of spontaneous division, that is there had already commenced in it the formation of a lateral, per-

[27]See e. g. Balbiani: Recherches expérimentales sur la mérotomie des infusoires ciliés. Recueil Zool. Suisse, t. V, no. 1, 1888. P. 48—49, 54; und Verworn: Die physiologische Bedeutung des Zellkerns. Archiv für die gesamte Physiologie, Band. 41. Bonn, Strauß, 1892. P. 13—14.

istomal, ciliated area, and he divided it in two halves. Since in this stage the chief nucleus, ordinarily moniliform, contracts into a round or bean shaped mass, Gruber was able to remove it completely from both halves. The division of the animal was effected in such a way as to produce about the same two halves as would later have been produced by spontaneous division. In the fragment which contained the original peristome the simple cicatrization of the wound was enough to reproduce a complete individual. In the other fragment which contained the posterior extremity the wound closed in the same way and the anterior extremity continued its development until the peristomal area and the buccal spiral were completely formed.[28]

This result seemed to contradict the view that the formative action of a nucleus, as a developmental center for the unicellular organism, was exerted continuously throughout the whole duration of development. But the following considerations show that this premature conclusion is quite fallacious.

We should remember in this connection another observation of Gruber. He cut off from the anterior end of a Stentor a fragment absolutely without a nucleus, but containing a small portion of the peristomal band. The cicatrization of the wound was followed by the ordinary contraction of the fragment and thereby the small portion of the peristomal band was given the appearance of a complete Infusorian such as would be formed by regen-

[28]Gruber: Uber künstliche Teilung der Infusorien. Zweite Mitteilung. Biol. Centralbl. Band, V, No. 5; May 1, 1885. P. 139—140; und: Beiträge zur Kenntnis der Physiologie und Biologie der Protozoen; Berichte der Naturforschenden Gesellsch. zu Freiburg i. B., Freiburg i. B., Mohr, 1886, P. 13—14.

eration. But that this was not actually the case was demonstrated by more careful observation by which it was recognized that the completeness was only apparent, for no part altogether lost was reproduced and no new mouth was formed in the place of the old one which had been removed.[29]

From this one could almost infer that some analogous phenomenon is the effective cause whereby the organs of the peristomal field, as soon as they are all formed in their essential parts, become arranged in the posterior anuclear half in about the same way as they would be arranged after the completion of spontaneous division.

Even if we admit a true and proper continuation of development, we must yet bear in mind first that it is not at all certain that this posterior half was completely deprived of macro- or micro-nuclear substance. For the micro-nuclei sometimes attain the number of fifty-four or sixty-six in Stentor coereleus, and it is always difficult to see them, especially in individuals in process of spontaneous division.[30]

Secondly we must above all things get a clear understanding of what the remaining alive for a while of anuclear fragments of adult individuals can signify, keeping in view at the same time the absolute generative incapacity of these fragments. They signify nothing else than a posthumous persistence for a while of the special action or series of actions, partly simultaneous, partly succes-

[29]Gruber: Uber Künstliche Teilung der Infusorien. Zweite Mitteilung. Biol. Centralbl., Bd., V. No. 5; May 1. P. 139—140.

[30]H. P. Johnson: A Contribution to the Morphology and Biology of the Stentors. Journal of Morphology, vol. VIII, no. 3. Boston, U. S. A., Ginn, August 1893. P. 499.

sive, which the nucleus was exerting at the moment of its excision or shortly before.

We can suppose, as we shall see better later, that this posthumous action of the nucleus ("Nachwirkung") may be explained in the following way: Each of the different nervous currents which the nucleus can discharge simultaneously or successively into the protoplasm deposits in it, of all the nuclear substances just that one which had given origin to it, perhaps by reproducing it partially while on its way. This substance once deposited in the protoplasm, would act as a reserve which, while incapable of growth by itself because it lies outside the nucleus, would nevertheless preserve for a time, until its gradual exhaustion, the capacity of producing the same current again. It would produce in relation to the excision of the nucleus, the same effect as would be produced by a very slow propagation of the respective current through the protoplasm.[31]

Therefore one can easily understand how in Gruber's experiment, in which the adoral ciliated zone of the animal was already in an advanced stage of formation, the whole series of simultaneous or successive formative stimuli had been already discharged shortly before the excision of the nucleus, and that therefore it remained only to await the slow unfolding of their effects, which would bring to completion the development already far advanced.

[31]Compare the partly similar, partly different hypothesis of Verworn on the posthumous action ("Nachwirkung") of the nucleus, which may be attributed to a reserve material built up gradually by the nucleus and given off to the protoplasm, and persisting till the protoplasm is used up, in the above mentioned article: Die physiologische Bedeutung des Zellkerns, P. 90; also: Die Bewegung der lebendigen Substanz. Jena, Fischer. 1892.

To one or other of these conclusions, either to the presence of an undetected micronucleus or to the posthumous action of the nucleus, one is necessarily driven, as we said, by the fact that only the nucleated fragments of an infusorian already completely developed, are capable of regeneration. For this capacity of reorganization, as one may call it, of the protoplasmic substance, which gives to it again the form of the complete individual but of correspondingly smaller size, cannot possibly arise either from the properties of this substance itself or from its specific "physiological units" for which the adult form of the individual would constitute the only state of equilibrium. This is quite impossible because a mass of protoplasm as large as the nucleated part, but which contains no nucleus, does not manifest the slightest tendency to regenerate, although it is capable of surviving its ablation for several days. The impulse tending to produce the specific form of the ordinary equilibrium is present only when the nucleus is not lacking.

Nevertheless the material which disposes itself in this definite specific form of equilibrium is not the nuclear material but the protoplasmic. The nuclear substance without participating itself in the process of reorganization, merely provokes it in the protoplasmic substance, which in this respect remains totally indifferent. This is demonstrated among other things by the observation of Gruber that the four nucleated fragments into which one individual was cut by a transverse and a longitudinal incision required in all cases the same time to regain their complete specific form including the adoral ciliated zone. The anterior end which already contained a portion of it and which one would suppose to be better adapted in its

protoplasm to this new formation requires just as long as the posterior end remote from the adoral zone.[32]

This impulse to reorganization which enables protoplasmic substance already organized to take on any other organization whatever speaks strongly in favor of the hypothesis that it is due to a special formative energy ("formgestaltenden Energie" as Nussbaum would call it) emanating from the nucleus, which using the protoplasmic substance merely as a support or vehicle or as an indifferent constructive material, would be in reality the only quiddity which tends to dispose itself in that particular form, which constitutes for it the only possible system in dynamic equilibrium. For the reasons above stated we must think that this formative energy is probably nervous in nature.

This ontogenetic function of the nucleus which we see in unicellular organisms permits of very important deductions in relation to all organisms whatever. For the complicated unicellular organisms whose manifold organs have different and mutually independent functions, such as for example a Stentor coereleus or a Paramoecium caudatum, are not essentially different from pluricellular organisms, but on the contrary are comparable with them in all essential respects.

"Between the internal differentiations of a complex cell," says Delage, "and so between the body of certain Infusoria, and the organs of the pluricellular being there exists I think only a casual difference, which depends not so much on the requirements of the differentiation as on the size of the organism." [33]

[32]Gruber: Uber künstliche Teilung bei Infusorien. Zweite Mitteilung. Biol. Centralbl., Bd. V. No. 5; May 1. P. 138.

[33]Delage: L'hérédité et les grands problèmes de la biologie générale. P. 97.

"However great," says Whitman quoting Gruber "the difference between an infusorian and a highly organized animal it cannot be a qualitative one. We can assume that the same vital elements serve in both as the foundation, only in ever new combinations. This kinship declares itself very clearly in the correspondence of many organs of the Infusoria with those of the higher organisms. We mention only the membranellae of the Infusoria which are quite similar to the corner cells of the mollusk Cyclas cornea." [34]

But we have already seen that when one cuts the infusorian into several nucleated fragments the membranellae can be formed from any given part of the protoplasm of the original individual, and can be arranged in definite relation to one another under the influence of the nucleus as a center from which the formative activity of the entire organism radiates. It is then probable that the formation and manner of disposition of the corner cells of the mollusk Cyclas cornea may be due also to a similar process of centroepigenetic nature. But this justifies us in suspecting that in all pluricellular organisms whatsoever, every formative process commencing with normal ontogeny is of centroepigenetic nature.

This hypothesis is supported for example by the experiments of King upon regeneration in Asteria vulgaris. These have given among others the following results: each of the arms cut off close to the body can remain living by itself for two weeks but is incapable of regenerat-

[34]Whitman: The Inadequacy of the Cell-Theory of Development. Biol. Lect. at the Mar. Biol. Lab. of Wood's Holl, Summer Session 1893; Boston U. S. A., Ginn, 1894. P. 118; and Journal of Morphology, Boston U. S. A., August 1893. Vol. VIII, No. 3, P. 651—652; Fig. 2 and 3.

ing the entire animal. If a fifth part of the body disc remains regeneration can occur in exceptional cases. If half of the disc is present the absent parts are always reformed.

If one amputates all five arms of the same animal by five transverse cuts, the first one very near the body, the others at four different distances from it, then after a certain time,—the same for all five arms,—the regenerated portion is largest for the first, and proportionately smaller for the other four according as the site of amputation was farther from the central disc.

This regenerated part which has developed from the amputated arm is much smaller in diameter than the original arm which was cut off. That is an indication that the regeneration is not produced by the cooperation of all the parts immediately adjacent to the surface of amputation.[35]

These experiments thus seem to indicate a distinct zone from which the process of regeneration proceeds and to the activity of which it is due.

From another side the existence of this formative central zone is almost required by the results of the similar experiments of Roux, which we have mentioned above, on the formation of half embryos of frogs.

These experiments show, in brief, that each half, right or left, anterior or posterior, can develop independently. If one admits also that this development is always entirely epigenetic in nature, that is that it is due entirely to correlative differentiations which the cells produce in one

[35]Helen Dean King: Regeneration in Asteria vulgaris. Arch. f. Entwicklungsmech. d, Org., Band, 7. Heft. 2. and 3. Leipzig, Engelmann. October 18, 1898. P. 351—361. Table VIII, especially Fig. 11.

another, it follows that at least each quarter of the embryo must have its own system of correlation networks independent of the other quarter systems. But the four quadrants have one zone which is common to all. Consequently at least these four independent systems of correlation networks for the four quadrants must come off from this common zone.

This suffices to warrant the statement that this latter must belong to a central zone of development, in the sense which we have set forth above; and that from this zone must branch off and diverge independently of one another the different great correlation networks or principal branches for the general distribution of nervous energy. These latter divide further into progressively smaller ramifications, one could almost say just as the great arterial trunks coming off from the heart continually subdivide down to the terminal capillary vessels.

It is nevertheless advisable to study these phenomena more closely. We must postulate that each of the two blastomeric nuclei obtained in the frog's egg after the first segmentation, when it once becomes completely isolated, is capable of giving rise to a complete embryo. But in the experiments of Roux, the disposition of the nutritive yoke or deutoplasm in the uninjured blastomere remains, thanks to the retention of its place by the injured blastomere, the same as the disposition which would have existed in this same blastomere if development had proceeded normally. Therefore, of all the specific potential energies which the uninjured blastomeric nucleus would be capable of activating successively, there would commence and continue to be activated only those which in normal development would have flowed directly into the

half of the egg affording such a definite deutoplasmic disposition.

So it becomes clear that when once the development of the uninjured half of the egg has commenced, the central zone concerned, even though it may be exactly the same as in the complete embryo, would activate only the specific potential energies proper to the corresponding half embryo and would produce only a half formation.

This half formation no matter how independent the great correlation networks might be, could nevertheless at each instant of its development, render the system of nuclear actions and reactions an incomplete one, without equilibrium, because at the plane of separation there would not be opposed to its own nervous tensions any equivalent system of tensions of the absent half. This incomplete system of nuclear tensions, not of itself in equilibrium, could nevertheless be prevented, even though only transiently, from equilibrating itself normally, by the special distribution of the nutritive yolk and by the presence of the injured half of the egg, still placed opposite that which is developing. But as soon as the continual increase of energy in the nuclear system overcomes these artificial barriers, equilibrium is once for all upset and postgeneration will appear.

It is necessary nevertheless to note that some demimonsters which proceed almost to the completion of their development would seem on the contrary to indicate for this incomplete system of nuclear actions and reactions a practical equilibrium existing from the commencement and persisting through all the stages of development. The typical example of these demimonsters is the famous Hemitherium anterius which Roux so thoroughly describes. It is constituted by the almost fully developed

foetus of a half-calf, in which all the posterior part of the trunk was missing as if it had been removed by a transverse cut.[36]

However that may be, one fact which speaks in favor of the hypothesis that the nutritive yolk acts as a temporary dam to a system of nuclear actions and reactions not of itself of equilibrium, is that these half embryos can be obtained only from those eggs in which, as in the Amphibia and Ctenophera, the nutritive yolk is abundant. Whereas in the case of animals whose eggs are poor in nutritive yolk, and present cleavage cells that are almost identical, as in the Echinodermata and Ascidiae, either a complete organism develops at once from the isolated blastomere or postgeneration appears very early.[37]

Another fact which speaks in favor of this hypothesis is that toward the end of a spawning period when the vitality of the egg, and consequently also of the blastomeric nuclei, is lower, the formation of pure half embryos is much easier to effect.[38]

While thus, after exclusion of preformation theories one can say that the formation of half embryos is a direct proof of the hypothesis of a centroepigenesis with its ramifying, independent correlation networks, this hypoth-

[36] Wilhelm Roux: Uber die künstliche Hervorbringung „halber" Embryonen etc. Virchows Archiv, Bd. 114. Oct. 1888. P. 132. Gesamm. Abhandl. Zw. Bd. P. 442.

[37] Wilhelm Roux: Uber das entwicklungsmechanische Vermögen der beiden ersten Furchungszellen des Eies. Verhandlungen der Anat. Gesellsch. Wien, 1892. P. 55—56. Gesamm. Abhandl. Zw. Bd. P. 809—810.

[38] Wilhelm Roux: Die Methoden zur Hervorbringung halber Froschembryonen und zum Nachweis der Beziehung der ersten Furchungsebenen des Froscheies zur Medianebene des Embryo. Anatomischer Anzeiger, Bd. IX. February 1894. P. 257. Gesamm. Abhandl. Zw. Bd. P. 954.

esis becomes confirmed indirectly by a whole series of other facts which Roux also has described and commented upon with his customary carefulness.

Natural or artificial headless monsters for example, and in general all monsters lacking entire parts but otherwise normal, prove that no formative action or reaction is exerted by the head or by these other parts upon the rest of the organism.

They speak therefore in favor of a centroepigenesis with independent networks of correlation in which it is necessary to suppose that the formative action must stream out entirely from a center toward the periphery. In all these monsters of which some part is lacking, there need be present only one part of the body namely the seat of the central zone of development.

Roux in his researches upon the formation of half-embryos once observed, as an example of the disturbance of correlations of mass by the absence of one embryonal half, a lateral dislocation of the notochord and a corresponding retardation of development of the dorsal part of the endoblast lying near the median line as marked by the semi-medulla and by the ventral parts. "It is an interesting fact," he remarks, "that the axial parts can be laid down and developed with so considerable a shifting in relation to one another. For this indicates further that the development of many parts even of the main parts is not included in the form as such; the embryo does not live a *formal* life." [39] These facts would also confirm the hypothesis of independent networks of correlation, the displacement of whose material would not alter their

[39]Wilhelm Roux: Uber die künstliche Hervorbringung halber Embryonen etc Virchows Archiv. Bd. 114. October 1888. P. 132. Gesamm. Abhandl. Zw. Bd. P. 442.

respective formative capacity, because it would leave unaltered the reciprocal relations of the different parts in each network.

Further, the deformations which the entire organism, and consequently also each of its different networks, undergo, would not seem to alter markedly the internal, reciprocal relations of the different parts of each network; thus from frog's eggs which had been compressed continuously during their development, the blastula and gastrula having been forcibly flattened, folded, and bent, there developed embryos whose internal and external aspect was just the same as though they had been allowed from the first to develop in a normal fashion and had undergone the deformation only later.[40]

"In the development of frog's eggs it happens very often," Roux writes further, "that the primitive mouth of the gastrula is not yet closed when the medullary folds appear, and this condition can persist in part up till the time of the closure of the medullary tube and the formation of the branchial elevations and adhesion cups. The formation of these latter can proceed in a manner which appears quite normal in the anterior half of the body even though the posterior half of the body may have quite an abnormal form, the primitive mouth remaining persistently wide open. Another instance, yet more surprising, is that in which notwithstanding the entire absence of the medullary ridges, the gastrula gradually exchanges its round form for a pear shaped one, a thing which ordinarily occurs only after the formation and development

[40]Wilhelm Roux: Uber die ersten Teilungen des Froscheies und ihre Beziehungen zu der Organbildung des Embryo. Anatomischer Anzeiger, Band VIII. 1893. N. 18. P. 608—609. Gesamm. Abhandl. Zw. Bd. P. 926.

of the medullary tube. These modes of behavior and others like them indicate that the parts which continue to develop normally require for their development neither the absent parts, nor that the remaining parts should be at the stage of development normally corresponding, and thus that they can develop alone, independent to a corresponding extent of those absent or backward." [41]

"Anachronisms of development," continues Roux in a later research, "appear also in the relative retardation or acceleration of development of one of the germ layers in relation to the others. For example several embryos otherwise normal, in which the medullary fold is still quite undifferentiated, show already in the mesoderm, in the entoderm, and in the chorda dorsalis, formations which appear normally only about the time of closure of the medullary tube. In this case there is an evident retardation of development of the ectoderm in relation to the development of the other two layers. There occur also inequalities of lesser degree in the rapidity of development of the two lateral halves of the body, and thus it is possible to observe two different stages of development in the same object." [42]

"If such large parts of the organism," concludes our author in a still later study, "can remain behind in their development or indeed remain absent, without thereby producing any disturbance in the development of the others, it follows surely that the development of these

[41]Wilhelm Roux: Zur Orientierung über einige Probleme der embryonalen Entwicklung. Zeitschrift für Biologie. Bd. XXI. München, Jul 1885. P. 478—479. Gesamm. Abhandl. Zw. Bd. P. 203—204.

[42]Wilhelm Roux: Uber die künstliche Hervorbringung halber Embryonen, usw. Virchows Archiv, P. 128—129. Gesamm. Abhandl. Zw. Bd. P. 438.

latter is not at all bound up by reciprocal actions with the absent parts, and also that it is not accomplished by the reciprocal action of parts of the whole organism." [43] These conditions are just those existing in a centro-epigenesis with ramifying and independent networks of correlation.

The formation of double monsters with double symmetry in the disposition of their organs is particularly in accord with centroepigenesis. Concerning this Roux expresses himself in this way: "In these double formations the fragment which is lacking in a symmetrically similar manner from each of the two individuals, can be any selected piece limited by a plane surface; and in them the organs are nearly all present and normal in form up to the plane of union, as if from two embryos, fully developed and ready to be born, one had cut off two symmetrical pieces so as to leave plane surfaces, and the twins had then been reunited by the cut surfaces." "The simultaneous development of two formations so extensively united, into two distinct bodies, of which each is centered in itself, indicates directly that there are not any general reciprocal actions operating to combine them into a single whole." [44]

According to the centroepigenetic hypothesis, the formation of these monsters would be due to the fact that the two blastomeres concerned, which are quite identical with each other since they arise from the segmentation of one and the same egg, have become, on account of ab-

[43] Wilhelm Roux: Uber Mosaikarbeit und neuere Entwicklungshypothesen. Anat. Hefte, Edited by Merkel and Bonnet, Februarheft 1893. P. 320. Gesamm. Abhandl. Zw. Bd. P. 859.

[44] Wilhelm Roux: Uber Mosaikarbeit etc. Anat. Hefte, P. 320. Gesamm. Abhandl. Zw. Bd. P. 859—860.

normal circumstances which have made them independent of each other, two distinct nodal points,—two central zones of development. The necessary consequences of the independent action of these two centers of development would be the centration of each individual by itself. On the other hand, the similarity of the two first blastomeric nuclei, which through multiplication give rise to both of the two central zones concerned, would bring about a similarity of the formative actions given off from these zones. Therefore those formative stimuli which act upon all points of any one of the infinite number of planes symmetrical in relation to these centers, would offset and annul one another, because they would be equal and opposite but only in so far as they do act along these planes. In this way could be explained why the parts lacking in both individuals must always be alike.

While thus all these different facts which have attracted the careful attention of Roux and been made the special object of his studies confirm, some directly others indirectly, the hypothesis of centroepigenesis with ramifying and independent networks of correlation, a further support, indirect indeed, but nevertheless very real, will be brought forward in the following chapter. For we shall endeavor there to show that if a whole series of facts compels us to throw over preformation, a series of other facts forces us to throw over simple epigenesis also, and this would give a high degree of probability to any other hypothesis with which both series of facts should be in accord.

Finally, the symmetrical disposition which the greater number of organisms present in relation to a point, to a straight line, or to a plane, and also the advance of growth along diverging ramifications, which indeed is a

general law of organic development, are phenomena which indicate in their turn that this centroepigenesis with ramifying, independent networks for the distribution of nervous energy, is also in harmony with the most general biologic phenomena.

One could always bring forward the objection that it is difficult to conceive how this series of energies acting one after the other, all upon the same point of the developing organism, could give rise to a series of dynamic systems of distributions as complex as we must necessarily suppose those to be which constitute the successive stages of ontogeny. To dissipate all doubts in this matter one may draw attention to the following simple hydro-dynamic experiment.

Let us imagine a very large cylindrical glass container almost filled with water, and having a hole at a selected point in the bottom of it. By means of a suitable force pump let us make more water enter the vessel through this hole with a velocity varying from one moment to another. To make the idea clear and the phenomenon more intelligible let us suppose that the velocity varies sharply each second, sometimes increasing, sometimes diminishing very considerably. On account of the great amount of water already contained in the vessel, the series of successive systems of very complex currents which will be produced each moment by the incoming water, whose newly added mass interpenetrates and displaces the other in a manner which we can make apparent in part by previously coloring the water to be injected, will depend on the entire series, and exclusively on the series, of different velocities with which the water is forced into the container.

A given series of dynamic actions, qualitatively alike

but quantitatively different, starting successively always from the same point could thus give rise to a succession of dynamic systems of as complex a configuration as one could imagine. Different series, that is to say those in which quantitative variations of the same dynamic action succeed one another in different ways, would naturally give rise also to dynamic systems of different configuration.

We can compare, though only roughly, this water which enters the container always by the same opening and with a velocity changing every instant, to the series of nervous currents of different specificity which, according to our hypothesis, would be discharged into the soma in the course of development, or into the great mass of yolk, by the activity of the germinal substance, always from one and the same point of the organism, which would thus constitute the central zone of development.

It would be proper at this point to touch upon the probable location of this central zone. But important as it is we do not need to stop long over it.

It is necessary at the outset to notice in a very general way that in plants, and especially in the higher plants, one must regard the leaf as the true individual and one must attribute to it a centroepigenesis of its own. The flower would then be merely the product of numerous centroepigeneses not entirely independent of one another: The corresponding simultaneous or rapidly successive activations of multiple centers, and the reciprocal action of these centers upon one another, would be indeed the agents by which modifications of each of the centroepigeneses is effected, so as to produce for example here a petal and there a pistil instead of an ordinary leaf.

It would also be possible for a center or a definite

group of these centers, perhaps on account of some special situation, to become, in the course or at the end of the particular centroepigenesis producing the different parts of the flower, and in relation to all the other centers and so to the whole flower, the director to a further development; so that there would be present for the whole development of the flower, or for a part of it at least, a centroepigenesis of the second degree.

By analogy one can conceive also of the possibility of other centroepigeneses of still higher degrees (composite flowers, etc.).

"It may appear," writes Le Dantec, "that the sexual individual belongs to a higher order than the asexual individual and may originate from the individualization of an association of parts which are like asexual individuals. It occurs perhaps in the Medusae; it is certain in Phanerogams. A flower corresponds morphologically to an assemblage in a fixed form, of parts which are like the asexual individuals of the plant. Goethe had already noted this peculiarity. The asexual individual of a plant is the internode with its leaf and auxillary bud: flowers are much more complex." [45]

Centroepigeneses of a second or higher grade could thus serve to explain the transformation of simple colonies of individuals, (e. g., of the ancestors of the present echinoderms), into complicated organisms, which tend steadily toward an individualization of their own. One could explain easily the transformation, for example, of the original individuals of the colony, becoming more and more differentiated from one another, into the organs of this organism (siphonophores). With the growth of

[45]Le Dantec: Traité de Biologie. Paris, Alcan, 1903, P. 413.

centralization (annelids, arthropods), centroepigeneses of the second or higher degrees would approximate gradually more and more the simple centroepigeneses of the first degree.

"The gastrula," adds Le Dantec further, "itself a morphologic unit of higher order than the cell, can itself bud off other gastrulas, just as the cell can produce other cells by budding. This budding may take place always in the same direction and so give rise to linear associations of gastrulas, as in the worms, arthropods, etc.; or it may take place in every direction and thus produce plant-like associations, for example the fibroid polyps or coral polyps; it may proceed radially and so give rise to the echinoderms. Even the vertebrates themselves would be, according to this, the result of an individualized assemblage of a linear series originally comparable with an annelid worm. That is the theory of human polyzoism of Durand de Gros and Edmond Perrier." [46]

After what has been said thus far the probable location of the central zone of development of the various types of organisms need not be especially treated of here.

The place in which we must suppose it to be, which naturally lies in the plane of symmetry of the organism, appears almost self evident from what we have said above, and will become steadily clearer from what will be said in continuation. It may here be remarked merely that this zone cannot be imagined as any special tissue marked off distinctly from the surrounding somatic tissues; but must rather be a simple, indistinguishable part of some tissue whose special, somatic functions in the adult individual are such as predispose it best, in the

[46] Le Dantec: Traité de Biologie. P. 412.

descendant organism, to the definite function of development, and which differentiates itself gradually from the other parts of this tissue by quite inappreciable and gradual transitions.

We have already said that the centroepigenetic hypothesis makes it necessary to distinguish the effective germinal zone, or true place of origin of the germinal substance, from the apparent germinal zone, which would be nothing else than the receiving station for the substance separated out or secreted by the effective germinal zone, or the place where the sexual cells concerned are built up out of this material. While we must regard only the effective germinal zone as the central zone of development, it is clear that the apparent germinal zone can be located at any part whatever of the organism.

In the higher plants the apparent germinal zone of the asexual budding cells, and that of the female, sexual cells, would seem generally to coincide approximately with the actual zone, that is, with the corresponding central zone of the leaf and of the flower.

In this way can be explained the heretofore puzzling phenomenon of the Xenia, in which as is known the flower after a hybrid fecundation, often takes on the form, size, color and tissue structure, characteristic of the variety from which the pollen comes; that is, as Darwin has already observed "in which the male element not only influences the germ as is its proper function, but at the same time influences various parts of the mother plant, in the same manner as it influences the same parts in the seminal offspring from the same two parents." [47]

[47]Darwin: The Var. of Animals and Plants under Domestication. Eighth impression of the second edition. Vol. I. London, Murray, 1882. Chap. XI, P. 433.

In the pluricellular animals we can start out with the simple supposition that if a central zone of development is present, it is probably that in which the blastomeres multiply with unlike rapidity; that is, it will be constituted by these blastomeres which multiply most rapidly. For this greater rapidity would in the majority of cases indicate a greater vitality or energy, which may be produced by a richer protoplasm or by any other special condition favoring the nutrition. And this greater energy would bring it about that the cells possessing it would win the upper hand over the others.

"The zone," writes Oscar Hertwig, "where the smallest embryonal cells lie, which are also those which divide most rapidly, becomes the place of gastrular invagination; it becomes something like a fixed center of crystallization for the animal development." [48] But these blastomeres are those which, in the vertebrates for example, later constitute the medullary tube and afterward the spinal cord.

As we shall see, everything seems to lead to the conclusion that in animals with specialized nervous systems the central zone is constituted by the least differentiated part of the nervous system itself; in the vertebrates probably by the innermost periependymal part of the spinal cord. This part after completion of its activity in determining development would, on account of the somatic function pertaining to it, likewise constitute the place where the infinitely manifold nervous activities of all the rest of the nervous system or rather of the whole organism are faintly re-echoed.

As we have already said, this location of the central

[48]Oscar Hertwig: Zeit- und Streitfragen der Biologie. Heft. 2. Mechanik und Biologie. Jena, Fischer, 1897. P. 180.

zone is almost self-evident from what has preceded, and will be still more so from what is to follow. Here it may only incidentally be remarked, (since we have treated of the subject more thoroughly in another place), that this hypothesis concerning the location of the central zone in vertebrates, and in general in those animals which have a specialized nervous system, finds a very strong support also in the numerous researches and observations upon the influence which the nervous system exercises upon development and regeneration.[49]

From this we can now pass on to the discussion, even though very briefly, of the question of the probable composition and structure of the substance which constitutes this zone, and which is consequently none other than the germinal substance. This affords an opportunity of speaking of the not essential but subordinate difference by which the germinal nuclei are probably distinguished from the somatic.

2. *Hypothesis Upon the Structure of the Germinal Substance*

We have seen that according to the centroepigenetic hypothesis, ontogeny can be attributed to a series of mod-

[49]See e. g. Wolff: Die physiologischen Grundlagen der Lehre von den Degenerationszeichen. Virchows Archiv, Bd. 164, 1902;—Richard Rubin: Versuche über die Beziehung des Nervensystems zur Regeneration bei Amphibien. Archiv f. Entw.-Mech. d. Org., Bd. XVI, Heft 1; March 13, 1903;—Kurt Goldstein: Kritische und experimentelle Beiträge zur Frage nach dem Einfluß des Zentralnervensystems auf die embryonale Entwicklung und die Regeneration. Arch. für Entw.-Mech. d. Org., Bd. XVIII, Heft 1; February 26, 1904;—Eugenio Rignano: Die zentroepigenetische Hypothese und der Einfluß des Zentralnervensystems auf die embryonale Entwicklung und die Regeneration. Arch. f. Entw.-Mech. d. Org., Bd. XXI, Heft. 4; September 11, 1906

ifications in the general distribution of nervous energy of the organism. If we consider the law of Haeckel in its first degree of approximation, we must suppose as we have already said, that this distribution of nervous energy constitutes by itself at each ontogenetic stage a system in dynamic equilibrium, because the same distribution of this energy was in equilibrium in the corresponding ancestors. To provoke the transition from one dynamic system to the other, it is necessary that at each ontogenetic stage there become active in the central zone a new specific energy, which disturbs the dynamic equilibrium which has just been formed and effects the transition to a new dynamic equilibrium.

This leads to the supposition that the germinal substance may be constituted by a number of material particles of which each would be able to activate only the corresponding specific nervous energy. We can designate each of these particles by the term *specific potential element.*

We must here provisionally postulate the possibility that there may be substances capable of containing in the respective potential condition, not only definite forms of energy but also different specific modes of the same form of energy. We shall take up the question again later in order to make it clearer and to handle it more thoroughly. It may be remarked here, however, that a chemical analysis of the material particles of the nucleus, which actually contain the hereditary mass, could hardly throw much light upon the eventual differentiation of the different materials which compose the entire germinal substance. For, at least for the moment, it can give only the composition of the possibly homogeneous residue into which

all these different substances break up or decompose as soon as life has gone out of them.

In conformity with the views of most biologists, we can assume that the hereditary mass, and therefore all the specific potential elements, are preserved and distributed during what is called the resting stage, in the granules of chromatin which are disposed like the beads of a rosary upon the nuclear reticulum; but during mitosis, in the chromosomes, and particularly in the little discs of chromatin which the chromatic filaments into which the nuclear reticulum and its granules contract, often present, superimposed upon one another and separated by intervening layers of linin.

We must nevertheless note that this mode of disposition of the different specific potential elements in the nucleus is of importance to us only in relation to nuclear division. For we must hold with the epigenesists, as we shall see soon, that this division always proceeds in a manner qualitatively the same.

But this disposition is of absolutely no importance to us in relation to the effects which it will have upon the serial activation of these elements. From this latter point of view we can indeed suppose these elements to be scattered through the germinal nucleus and mixed with one another in any way whatever.

For, as we shall see better later, the activation of every specific potential element in the proper ontogenetic stage, depends in no way upon its position in relation to the others, but rather on the condition that at this stage only its activation requires the doing of only a moderate amount of work—an amount which does not require more energy than the total quantity inherent in each element. Its activation in any other stage would require, on ac-

count of the much greater modification which it would then induce in the distribution of nervous energy already existing, the doing of a large amount of work,—an amount which would require more energy than the quantity present in each element.

The centroepigenetic hypothesis of a single limited zone containing the germinal substance, and the other conception following upon it, that the germinal substance may consist of a number of different, material particles, each representing one particular, specific, potential element brings up the question of nuclear somatization.

We postulate the existence of a central germinal zone distinct from the soma. We must not forget nevertheless that all nuclei arise by division from the first, that of the egg. If we also admit with the epigenesists a qualitatively equal nuclear division, then the nuclei destined to become somatic must at first be equivalent with those destined to become the central zone of development. In what way then is the nuclear somatization brought about in the cells which later must constitute all the different tissues of the body?

There presents itself at once the preliminary question: Must we really admit this nuclear division to be always qualitatively equal? Or shall we rather hold with the preformists that in addition to equal nuclear divisions there may be also unequal divisions? On this point we believe we ought to agree unconditionally with the epigenesists.

There does not exist any observation which gives even the slightest ground for the conclusion that there is a qualitatively unequal division. "By the most thorough study of the longitudinal division of the chromosomes,"

writes Strassburger, "it is absolutely impossible to hunt out anything but equal division. Unequal division is not presented at all. There is not a single fact to support the notion that it exists." [50]

We shall here limit ourselves to mentioning only two orders of facts which speak directly against unequal division:

First, it does not occur in any nucleus in the vast realm of unicellular and of primitive pluricellular forms, consisting of colonies of like cells; for in them the facts of heredity show directly that nuclear division is always equal.

But especially the oft repeated and keenly discussed experiments upon the relative shifting and isolation of blastomeres afford direct proof that nuclear division is equal in the first segmentations of the egg. We recall for example the experiments of Chabry upon the Ascidians, those of Wilson upon Amphioxus, those of Herbst on the separation of the blastomeres of the sea urchin merely by adding chloride of potassium to ordinary sea water, of Driesch on the Echinus microtuberculatus, of Oscar Hertwig upon frogs' eggs, of Raffaello Zoja on the Medusae and so on. These experiments in which one of the first blastomeres, or one of the four, or eight, or sixteen, or thirty-two first blastomeres, produce when isolated an entire embryo, perfectly formed but proportionally smaller, or in which the blastomeres, though shuffled about in any way whatever, nevertheless developed in a perfectly normal way, lead with the greatest certainty that any one could desire to the conviction that in the

[50] Straßburger: Uber periodische Reduktion der Chromosomenzahl im Entwicklungsgang der Organismen. Biol. Centralbl., XIV. No. 23-24. Leipzig, Dec. 1, and 15, 1894. P. 835.

successive blastomeric divisions the nuclei always remain like the first, that of the egg from which they sprung.

The contrary cases of the formation of half embryos, or of incomplete embryos, after the separation or killing of one of the two first, or of several of the first blastomeres, are found always and only in embryos rich in deutoplasm, so that, as we have already seen, they cannot afford any ground for the conclusion that the nucleus or nuclei from which these incomplete embryos develop must be different from the first nucleus, that of the egg.

We shall examine in the following chapter the very complex and untenable subsidiary hypotheses, to which the partisans of unequal division have been driven, in order to bring their principal hypothesis into accord with experiments upon the isolation and displacement of blastomeres, and also with other equally irreconcilable processes, such as post-generation and regeneration. Here we shall only quote and adopt the conclusion which Oscar Hertwig has drawn from these experiments, namely: "It is self-evident that such an interchange of blastomeres without injury to the product of development, is possible only if one nucleus has the same characters as the others, that is, only if all the nuclei are produced from the segmentation nucleus by hereditarily equal division." [51]

In order that this hereditarily equal division may be materially possible in a germinal nucleus constituted by innumerable, different, infinitely small particles,—that is in order to permit the division of each of these particles or substances between the two daughter nuclei,—it would be sufficient that they become disposed during mitosis in little transverse layers one over another in the various

[51]Oscar Hertwig: Die Zelle und die Gewebe. Zw. Buch. P. 69.

little discs of chromatin of the chromatic filament, in exactly the same disposition as that which these little discs actually do present in the chromatic filament.

Admitting then that nuclear division is always qualitatively equal we must now ask: does this really mean that the nuclei of all cells must remain alike throughout the whole of development?

But before taking up this question we must first answer a preliminary one: must we exclude nuclear somatization with the epigenesists or admit it with the preformists?

If it seemed to us impossible to disagree with the epigenesists upon the first question of a qualitatively equal nuclear division, it seems on the contrary impossible to disagree with the preformists on this second of a nuclear somatization. We shall certainly not repeat here all the arguments by which these latter support their thesis. They can be summed up in their essential parts in the following words of Weismann.

"The chromatin is able to imprint upon the cell in the nucleus of which it lies a specific character. Just as the thousands of cells which make up the organism possess very different characters and very different functions, so the chromatin which controls them cannot be every where alike, but must rather be different in different kinds of cells." [52]

The epigenesists, on the contrary, are well known to be inclined to the view that all the somatic cells of the organism have, without distinction, like nuclei constituted by the same idioplasm. Oscar Hertwig indeed ventures the assertion that each somatic cell if it were

[52] Weismann: Das Keimplasma, eine Theorie der Vererbung. Jena, Fischer, 1892. P. 43 and 268.

possible to put it in conditions which would render it capable of nourishing itself and preserving its life independently separated from the rest of the organism, could function as a germ cell.[53]

And certain processes which appear in all the lower organisms, with tissues that are not very highly specialized, appear to justify this view.

If one places a piece of a Begonia phyllomaniaca in some earth in moist air, after cutting through the leaf-ribs in different places, one finds after some time, in the neighborhood of each wound, one or more little new plants. Any fragment whatever of a hydra or medusa possesses the power of reforming an entire animal without increasing its mass, but rather by a process of differentiation and rearrangement of cells already existing.

A theory which admits equal nuclear division and also a slow and gradual nuclear somatization, resulting from the action of a determinate zone constituted only by the germinal substance, would reconcile the different and contradictory phenomena brought forward by the epigenesists on the one side, and by the preformists on the other.

Oscar Hertwig who as we have just seen is a zealous partisan of the idioplasmic equality of all nuclei, is committed in another place to the possibility of a certain nuclear somatization. "The hypothesis of a hereditarily equal nuclear division does not imply the view that the 'anlage' substance must therefore be an immutable thing. . . . The idioplasms of certain groups of cells of an organism which find themselves permanently in unlike conditions in consequence of their different spatial and functional disposition in the body as a whole, dif-

[53]Oscar Hertwig: Die Zelle und die Gewebe. Zw. Buch. P. 304—305.

ferentiated as it is through the division of labor, can receive to a certain extent the stamp of local character."[54]

If we admit that each new specific current while passing through a nucleus deposits there the substance which was capable of producing it, and which would be capable on occasion of reproducing this same specific current,—a hypothesis of which we reserve a better exposition till later,—we can conceive of nuclear somatization as a gradual and constant acquisition of new, specific, potential, somatic elements.

The fact that each cell, as long as its differentiation has not progressed too far, can upon occasion, provided it be isolated from its neighbors, arise to the rank of a germinal cell, appears to indicate that these new somatic elements, thus gradually acquired, would from the start be simply added to the germinal elements already existing, without altering them at all, but merely relegating them to the potential state, from which, under normal conditions, they would not again emerge.

In other terms we must suppose that all the germinal elements remain unaltered in the nuclei undergoing somatization as long as the number or the mass of acquired somatic elements does not progress beyond a given limit.

But when this limit is once passed, then the requirements of nutrition or of space would cause the different germinal elements to disappear gradually, and the nucleus concerned would thus lose all generative capacity.

Further even those somatic elements, which each nucleus acquired one after another at each successive stage of development, will gradually disappear after

[54]Oscar Hertwig: Zeit- und Streitfragen der Biologie. Präformation oder Epigenese? Jena, Fischer, 1894. P. 142—143.

ontogeny is completed, for then the nuclei are always exposed to one specific current or to a limited group of specific currents peculiar to the adult state. There would remain over only a small or very inconsiderable number of those somatic elements which were acquired last and which would thenceforth continually increase in mass. The cell would thus lose by degrees its undifferentiated embryonic aspect, and its exclusively somatic characters would steadily increase.

While according to Weismann there would be a fundamental distinction between the germinal nuclei set apart for the preservation of the entire hereditary mass, and the somatic nuclei which from the first would receive only such particles of that hereditary mass as are indispensable for their function, and the ontogenetic passage from one to the other would take place suddenly and directly at the very commencement of development; according to the centroepigenetic hypothesis, on the contrary, there would not exist any essential difference between them, because they differ from each other only in the number and the specificity of their respective potential elements, and the passage from one to the other would be effected gradually and slowly. And this transition would be due we repeat only to the constant acquisition by the nuclei destined to become somatic, of new specific potential elements, which at first are simply added to the germinal elements already present but finish by causing the latter gradually to disappear on account of the requirements of nutrition and space and by taking their place themselves.

Without needing to have recourse to a reserve idioplasm, or to any other equally involved subsidiary hypothesis, one can explain in this way the phenomena,

common in plants, of the retention by some cells of the germinal capacity even though they belong to somatic tissues which have already advanced to a certain degree of differentiation.

In the same way is easily explained how a given piece of a hydra or medusa reorganizes itself so as to reproduce the entire individual without any corresponding increase of its mass.

For since histologic differentiation in the hydra is not very pronounced one can surmise a priori that in all or nearly all their cells, the whole of the specific potential elements must coexist with the somatic elements peculiar for each cell and acquired by it during development. The separation of the fragment from all the rest of the organism, which arrests the general circulation of nervous energy, will therefore cause the somatic elements which were active in the intact individual to return to the exclusively potential state and thus enable the germinal elements to become active again. That cell or group of cells which surpasses the others in vigor will have its germinal elements activated first and will then form a central zone directing development of the others; and the distribution of nervous energy, which again passes through the wonted series of ontogenetic stages, will now proceed in the fragment in the same way as formerly in the entire individual.

There are often external circumstances which determine what cells of the fragment shall constitute the central zone. Thus if one cuts off from the trunk of the hydra both the tail end and the head end at the same time, and then places the fragment with the lower cut surface down, the head is reproduced at the same end as formerly, whereas if one turns it over so that the former head end

of the polyp sticks into the sand of the aquarium, the head is reproduced at the aboral pole.

Sometimes two distinct groups of cells seem to struggle with each other to constitute the central zone of development, and both may attain their object thus producing double monsters. If from the trunk of a hydra one cuts off at the same time both the tail and the head end, and suspends the fragment horizontally in the water it forms a head at both ends.

In an analogous way, Morgan in his experiment on the regeneration of Planaria maculata once obtained from a fragment which had been cut off by two transverse sections, two heads one at the front end, the other at the hind end.[55]

This simultaneous activation of two centers of development can go on also at the commencement of ontogeny in the cells of the blastula itself. "From causes which are yet beyond our knowledge, there are often produced (in fish eggs) two gastrular invaginations instead of one, at separate points of the blastula. And it depends on the position of these two invaginations, which could also be designated crystallization centres for the further development of the embryos, how the embryonic cells of the germinal disc are then drawn into the process of development, given very definite positions in relation to one another, and utilized for the formation of organs." [56]

The analogous phenomena of heteromorphosis in general can likewise be explained, through the similar,

[55]Morgan: Experimental Studies on the Regeneration of Planaria maculata. Arch. f. Entwicklungsmech. d. Org. Bd. VII. 2 and Heft, 3. Leipzig, Engelman. Oct. 18, 1898. P. 381, 395.

[56]Oscar Hertwig: Zeit- und Streitfragen der Biologie. Präformation oder Epigenese? P. 60

abnormal activation of new centres of development after amputations, incisions, or in any other abnormal conditions whatever in the most different regions of the organism which otherwise would have continued to constitute definite somatic parts of it.

In Planaria maculata for example these new developmental centers of heteromorphous formations, of which this animal affords perhaps the most typical cases, appear, according to the results of recent researches, to be formed always from one of the two ends of the piece of the lateral nerve tract which is separated by the operation from the other parts of this tract.[57]

Indeed it appears to be indicated by these latest and most careful researches that those pieces of the planarian which contain no part of this nerve tract are not able to regenerate themselves, any more than are those fragments of infusoria which contain no part of the nucleus.[58]

Therefore this animal forms perhaps the transition from those pluricellular organisms in which all the somatic cells preserve throughout their capacity of regeneration undiminished, to those in which this capacity exists in the adult in only a very definite and special zone.

The phenomenon which more than any other speaks in favor of a nuclear somatization arising in the higher multicellular organisms during development, is the circumstance that the capacity of regeneration diminishes with age; for it is very much greater in embryos than in fully developed animals. For example, if the feet of an adult frog are cut off, they do not grow again, whereas

[57]Charles Russell Bardeen: Factors in Heteromorphosis in Planariae. Arch. f. Entwicklungsmech. d. Org. Bd., XVII. 1. Heft. 13 March 1903. P. 1—20, esp. P. 6—8; Fig. 5, 6, 7.

[58]Charles Russell Bardeen: Ibid. P. 2, 3.

Barfurth has demonstrated that during the first stages of development this regeneration is complete. And Roux has found that if one cuts quite young frog embryos into longitudinal or antero-posterior halves the missing parts are completely regenerated in a few hours.[59]

On the other hand, if the regeneration of the optic lens in the triton from a tissue other than that from which it is developed in ontogeny, is of itself enough to exclude preformation decisively, it is nevertheless not in any way incompatible with the most complete nuclear somatization. If one admits this latter, the histological transformation of certain cells would indicate only the possibility that in certain ways somatized nuclei may become differently somatized, if unusual influences are exerted upon them by neighboring nuclei, that is if nervous energies other than the usual ones act upon them; and they would undergo this new somatization through the gradual acquisition of new specific, potential somatic elements, different from the former ones. By itself this transformation certainly does not prove that all nuclei of the different cells consist of like idioplasm.

Further there is no firm support for this supposed idioplasmic identity of the nuclei in the researches dealing with vegetable and animal grafts.

In order to support such a hypothesis effectively, these investigations would have to show a closer relationship or "harmonicity" (as Vöchting would say) between different tissues of the same individual or of individuals belonging to the same species, than between like tissues

[59]Roux: Uber die verschiedene Entwicklung isolierter erster Blastomeren. Arch. f. Entwicklungsmech. der Organismen, 1895, Band, I. Heft 4. P. 614.

of different species. But this demonstration has not been afforded in a single instance of animal grafting.

There are indeed examples of transfusion of blood which do not succeed when they are made from one animal to another of different species, whereas they do succeed perfectly between animals of the same species. There are the experiments of Bert upon the successful transplantation of a fragment of the tail of a mouse into the subcutaneous tissue at another part of the body of the same individual or of another individual of the same or a related species, as Mus decumanus and Mus rattus, whereas such a transplantation is not successful between species farther removed, such as Mus rattus and Mus silvaticus. There are the experiments of Ollier and Schmitt on the transplantation of fragments of bony tissue, which were successful in transplantations from one part to another of the same individual or to another individual of the same species, but failed between individuals of different species.[60]

But all these experiments indicate only that there is more affinity between the parts of the same tissue or of similar tissues when they belong to individuals of the same species or of related species than when they are taken from individuals of different species. They do not prove at all that there is more affinity between parts of different tissues, which come from the same individual or from individuals of the same species, than between parts of the same tissue taken from different species.

On the other hand Joest's experiments have demonstrated the possibility of true heteroplastic grafts in the annelids, in which it is easy to obtain transplantations

[60]Oscar Hertwig: Die Zelle und die Gewebe. II, P. 24ff.

between different species. In contrast with the results obtained by Ollier and Schmitt, the transplantation to man of portions of bony tissue and of horny tissue which were taken from carnivorous or rodent mammals, has been entirely successful. It is known indeed that the transplantation of a cock's comb to a cow's ear has been successfully effected. Born, in his famous experiments, has succeeded in transplanting definite parts of young embryos of Rana esculenta to corresponding parts of other embryos, not only of the same species but also of different species (Rana fusca, arvalis and esculenta), and indeed of different genera (Rana esculenta and Bombinator igneus).[61]

All these experiments show that the plasticity or capacity of transformation of living organic substance reaches much farther than between individuals of the same species. Therefore it cannot be explained by the idioplasmic identity of the nuclei, which in any case could exist only between tissues of the same individual and between individuals of the same species.

There are certain grafts in plants that appear to justify the conclusion that there is a single nuclear idioplasm, identical throughout the whole plant. For in grafts between plants of the same species there has even been obtained the union of parts which have nothing in common with each other at all, as for example a root with a leaf. Whereas if one attempts to transplant even in quite normal relations, parts of plants belonging to

[61]Compare e. g. Oscar Hertwig: Die Zelle und die Gewebe. II. P 23; Delage: L'Hérédité etc. P. 114; G. Born: Uber Verwachsungsversuche mit Amphibienlarven. Leipzig, Engelmann. 1897. P. 146ff.

different species the result of the graft is not certain and often unfavorable.

This can be explained by the fact that in numerous species of plants, as we have seen, nearly all the cells preserve the reproductive capacity. What one calls "vegetative affinity" is then perhaps nothing else than a direct effect of the retention of the whole of the specific germinal potential elements in addition to the somatic elements peculiar to each of the different tissues, in all or nearly all the different nuclei which do not pass beyond a certain degree of differentiation.

In drawing a conclusion from all that has been said so far, we are confronted with this apparent paradox: on the one side, it seems that in conformity with the epigenesists we must reject a nuclear division which during one and the same development must be sometimes qualitatively equal, sometimes unequal, as inadmissable and refuted by the facts, and instead of this admit only a nuclear division always qualitatively equal. On the other hand it appears that in conformity with the preformists, one must likewise exclude a nuclear substance, identical in all the cells of the same organism, and must accept on the contrary, the hypothesis of an actual nuclear somatization. It follows that this nuclear somatization can be effected only gradually and only by a process of epigenetic nature.

But when one has once admitted equal nuclear division and gradual nuclear somatization by a process of epigenetic nature, there follows therefrom necessarily the hypothesis of centroepigenesis. For if the nuclei of the cells of the different tissues of the body finally become completely somatized it is certain that some certain ones of the nuclei constituting the organism do not become

somatized at all, namely those whose function it is to supply the reproductive cells with germinal substance. And if the first nuclei become somatized by a process of epigenetic nature, this process even though it involve the entire organism, must leave the other nuclei unaltered. But this would be possible only when this process is dependent on influences proceeding from the zone of germinal nuclei, and being exerted by it in such a manner that the germinal substance concerned does not become altered at all.

The continuity of the germinal substance, the specificity of the nuclei, and the epigenetic nature of the formative processes of organisms,—these three conceptions which individually are favored by a great number of biologists—imply together the conception of centroepigenesis.

Another fact which has been considered perhaps less than it deserves, supports the hypothesis that the process of development is not only of epigenetic nature, but also depends upon influences coming off incessantly and successively from a point which is external to all the transforming parts, but which remains itself unchangeable; namely the elasticity by virtue of which developing organisms, much more than those completely developed, are able not only to undergo without injury enormous changes of form but also to resume their original form as soon as the disturbing influence ceases. And just to this greater elasticity of the young organism is to be attributed the fact that it is much less plastic than the adult organism.

In fact the centroepigenetic hypothesis would permit one to deduce this a priori. For according to it the young organism is so much more elastic, because in it all the cells, being less specialized, are thus much more

easily able to assume any new somatic character whatever which may be imposed upon them. It makes no difference in the case of the still unspecialized cell, or even in that of the cell which is in the first stages of specialization, whether the somatizing stimulus is ontogenetic, proceeding by indirect ways from the central zone, or functional, induced by the environment. For the embryonic cell is in itself thoroughly plastic. Consequently the young soma would also be plastic if it were not continually influenced by the formative stimuli proceeding from the central zone of development. This influence though it is more feeble than the functional stimulus proceeding from the environment and consequently unable to resist it, has nevertheless the advantage of being continuously in action, and so of gaining the ground lost, as soon as the action of the environment ceases.

The cells of the adult soma are on the contrary less plastic, because they are already considerably specialized. But every modification which their limited plasticity permits in them remains, since the opposition of the central zone of development has already ceased. The adult organism is much less elastic. But in respect to the permanence of results it is more plastic than the young one.

And, as already said, this is entirely confirmed not only by the most commonplace phenomena, but also by the most careful embryologic researches. In fact considerable changes of form, which would be destructive to an adult organism are, on the contrary, very well borne by the young. But attentive observation of these processes shows us also, as stated, that the younger the organism the greater is its elasticity, which tends, when the disturbing action has ceased, to restore it to its

primitive state. Thus it is that a wound or a fracture is never so detrimental to the child as to the adult; but it is also true that with the same intensity and duration of the educative influence directed toward the modification of inborn tendencies the results are more permanent the older the child is.

This elasticity of development is proved by Roux with his customary care in the following way.

In one of his experiments on the effects of passive deformations in the first stages of development he succeeded in bending a few frogs' embryos within their gelatin envelopes by squeezing them between needles. "If the needles were removed immediately after the deformation, the embryo at once took on again its previous form; if they remained however a few hours the deformation tended to be a persistent one and disappeared again only in the course of several hours; a proof that an internal adaptation to the new form had already commenced, but which was in its turn caused to disappear in the course of further development, perhaps by the action of growth forces inhibited during the deformation but resumed upon the restoration of the normal form." [62]

Roux gives this dynamic elasticity of development the name "mechanism of self regulation." Let us note again that the absence of this elasticity in adult organisms, which remain plastic in relation to the somewhat persistent, deforming influences of the environment, would denote that this mechanism is active only during embryonic life. Now the continued action exercised by the central zone of development constitutes precisely such a mechan-

[62]Wilhelm Roux: Zur Orientierung über einige Probleme der embryonalen Entwicklung. Zeitschr. f. Biol. Bd. XXI. München, July 1885. P. 515—516. Gesamm. Abhandl. Zw. Bd. P. 245.

ism of self-regulation, active during the whole of ontogeny but ceasing upon the completion of development.

Another example of the dynamic elasticity of development, no less characteristic in certain respects than the preceding, has been repeatedly observed by Roux in the postgeneration of his half embryos. "In the postgeneration of the mesoblast it can be observed that very young yolk cells with nuclei not yet stainable, and also the remains of substances not yet cellulized, hinder the differentiation, and so divert the mesoblastic formation toward the interior or divide the formation into two layers; but after the circumvention of this obstacle the further differentiation soon resumes its normal course; a procedure in its essence extremely puzzling." [63]

It may be merely noted here that this elasticity of development helps to explain the interpolation of certain newer ontogenetic formations or stages (placenta and similar things) in the series of older ontogenetic stages, without markedly altering the earlier or later members or even the last member of this ancient series.

"We have reason to believe," says Orr, "that the manner of growth for some particular period of the development may be secondarily changed without radically affecting either the preceding or succeeding growth. As an example of this may be mentioned the embryonic organs and embryonic modifications which adapt the embryo to undergo partial development in the body of the parent, and allow it to receive nutriment from the parent, e. g. the placenta." [64]

[63]Wilhelm Roux: Uber die künstliche Hervorbringung halber Embryonen usw. Virchows Archiv. Bd. 114, October 1888. P. 276. Gesamm. Abhandl. Zw. Bd. P. 504.

[64]Orr: A Theory of Development and Heredity. New York, Macmillan, 1893. P. 210.

These embryonal organs and modifications which interpolate themselves in the series of ontogenetic stages, leaving these latter unchanged, can then also serve as proof that developing organisms are elastic but not plastic, while contrariwise grown organisms remain plastic but not elastic.

To these facts one can add that the large accumulation of yolk in the egg cells exerts a great influence on the first stages of development, but subsequently exerts absolutely no influence on the other stages. "The organization of the egg," says Hertwig, "which depends on the disposition of the deutoplasm, has fundamentally only a subordinate influence, and that of a secondary and transient nature in the developmental process." "Eggs of animals which belong to different races can present a very similar type of cleavage and similar early embryonic forms, while eggs from closely related divisions of one and the same race divide in very different ways, and differ very extraordinarily in the nature of the blastula and gastrula. The deposition of yolk material in the egg imprints a quite characteristic stamp upon the first embryonic stages,—the cleavage process, the blastula, gastrula and so on,—but it has no influence on the essence of the animal species itself, nor on the formation of any special species of animal." [65]

One has here then developments, which, altered in the first stages by the influence exerted by the yolk material, later resume their normal course, exactly as though they had undergone no alteration. In other words the yolk substance alters the normal development only temporarily, only for so long as its action continues to make

[65]Oscar Hertwig: Die Zelle und die Gewebe. II. P. 265—266.

itself felt. This process corresponds essentially to that described in the above mentioned researches on the transposition of the blastomeres, in which the latter were compressed for example between two plates and so all compelled to lie in the same plane. But when the pressure ceased they resumed at once their normal disposition. Each of these two processes constitutes another proof of the self-regulating capacity or elasticity of development which finds in centroepigenesis its most simple explanation.

Centroepigenesis implies further, as we have seen, that the distribution of nervous energy in each stage of development forms in itself a system in complete dynamic equilibrium, which becomes disturbed and replaced by another system in equilibrium, only through the activation by the central zone of a new specific potential element. This is the conception from which as a starting point we have built up our hypothesis.

It follows that if the activation of the specific potential elements successive to any given stage is prevented through certain abnormal circumstances, development will stop without thereby causing the organism thus remaining behind in an earlier ontogenetic stage, to cease to form a dynamic system in complete equilibrium.

Such transitory or permanent arrests of development are extremely numerous, much more numerous than commonly believed. All the phenomena called atavistic reversion belong in this category. Metamorphoses also, with the exception of certain characteristic and remarkable phenomena which have been added later, are only similar arrests of development, which proceeds at once on its course as soon as external conditions, and with them also

the conditions within the organism, become again favorable to further development.

As a typical example of these arrests of development may be mentioned the well known case of the aquatic salamanders, (newts). These tailed amphibians at a certain stage of their ontogeny take to the land, lose their gills, and become accustomed to respiration by lungs. If however they are prevented from doing that by imprisonment in a closed aquarium, they retain their gills, and the triton is halted for life at a low stage of development, which its near relatives, the perennibranchs never pass.

The hypothesis of centroepigenesis, which has thus been derived in its entirety from the fundamental biogenetic law taken in its first degree of approximation, that is in the sense of an exact repetition of phylogeny by ontogeny, implies also that in two species arising from a common ancestor, the series of specific potential elements remain the same up to the ontogenetic stage corresponding to this common ancestor, and only after this stage do the series of elements concerned in the two species diverge from one another.

It follows that in crosses development can go on very well so long as the two series of germinal elements are identical, but it becomes hindered as soon as the elements concerned, which strive to become active at the same time, thwart one another by their difference. And through this hindrance to development the organism will take on a form similar to that of the common ancestor. Further a few germinal elements too feeble heretofore in relation to the others, and therefore unable to become active during the development of organisms of the pure strain, are able, if common to both races, to acquire by their union a preponderance over the others different in the two species,

and so to secure the energy necessary to their activation, and thus to bring out in the cross certain characters of the ancestor which otherwise would not be found in the existing species in any of its ontogenetic stages.

In this way then, by the arrest of development at the ontogenetic stage at which the respective germinal elements of the two species begin to diverge from one another, can be explained in the most direct possible manner the above mentioned phenomena of atavistic reversion which all hybrids present.

"The offspring of a cross of two such species," writes Orr, "might therefore continue its development so long as the two inherited impulses were alike, but when the impulses begin to impel growth in opposite directions, development must cease. This explains why the imperfectly developed offspring of a crossed species resembles an ancestral form." [66]

For example the distinct, colored, transverse stripes on the foreleg and shoulder of the mule, which in the horse and the ass are quite rare and usually very faint, arise in this way and must be referred to the common ancestor of both species. From the crossing of certain races of pigeons arise birds which have the slate colored plumage of the wild dove, even though the races concerned in the crossing possess quite a different color. But it has been proven that these races branched off directly from the wild races. In the same way the mixed breeds of domestic ducks recall the wild ducks. And the hybrid of a German and Japanese pig is quite similar to a wild boar. The hybrids of Datura ferox and Datura laevis regularly have blue flowers instead of the white of their parents;

[66]Orr: A Theory of Development and Heredity. P. 230—231.

and Darwin proves that this is a reversion to a blue flowering ancestor. The tendency to incubate, which domestic hens so often lose, always appears again in their hybrids. The hybrids of ducks show a tendency to migrate. The mule is harder to break thoroughly than the horse or the ass.[67]

These examples afford, in our estimation, the most certain proof that the ontogenetic stimuli of two species arising from a common ancestor must remain alike during a long series of earlier developmental stages, and only in later stages begin to diverge from one another. And this is just what the centroepigenetic hypothesis implies, but what no other hypothesis has yet been able to explain.

Further the hypothesis of centroepigenesis teaches us that the series of like germinal elements must be shorter the farther removed the species are from the common ancestor. Now Morgan as is well known has obtained hybrids in which, for example, eggs from Asteria were fecundated by sperm from Arbacia, which belongs to the genus Echinus. The two parent forms belong here not only to two different genera but also to two different classes. But these hybrids have never got beyond the larval form, the pluteus which represents only one of the first stages of ontogeny.[68]

The hypothesis of centroepigenesis, finally, regards development as completed at the moment when all the germinal elements have achieved activation. We note that the central zone is then no longer required to employ its acquisitions of nutritive material for the growth of its

[67]Darwin: Animals and Plants under Domestication. II. P. 13—21: Crossing as a direct Cause of Reversion; P. 254.

[68]Morgan: Experimental Studies on Echinoderm Eggs. Anat. Anzeiger, Bd. IX. No. 5 and 6; Dec. 23, 1893. P. 151—152.

entire mass or for the restoration of the masses of any of its specific elements, as at the time when these latter were being used up in proportion as they became activated. And perhaps this explains also why the sex cells, which according to our hypothesis form only the container for the germinal substance given off by the central zone, usually become "ripe" only at the end of development.

When the continuous activation of new specific potential elements ceases, the disturbing influences exercised by the central zone upon the dynamic equilibrium of each ontogenetic stage will cease also. And thus the organism arrives at the final equilibrium of the adult condition. But now the functional stimulus in the widest sense of the term can come into play, with the innumerable variations possible for it, as new causes of perturbation.

So just as formerly the perturbing influence of the central zone upset the just formed equilibrium, and thereby provoked a transition to the next ontogenetic stage, so now each persisting alteration of the functional stimulus disturbs the dynamic equilibrium of the adult condition and thereby causes also a different distribution of the general nervous energy. Through each cell of the entire organism, or of definite portions of the organism, there will consequently flow a nervous current specifically different from that present before, and also specifically different from one cell to another.

There is formed and deposited therefore in the nucleus of each of these cells a particular specific potential element, which will add itself to the element or elements already present. But all the elements, the new as well as the old, which are deposited in the somatic nuclei will be lost with the death of the individual; and only those will be preserved from annihilation, which have been depos-

ited in the nuclear substance of the central zone. The permanent change of the functional stimulus will thus have as its result, in so far as the species is concerned, only the simple addition of a new specific potential element to the germ substance.

We must therefore now study in what way this new element behaves during the ontogenesis of the succeeding organism. But this investigation will form the object of one of the next chapters.

After we have thus brought to a conclusion this short review of the most important processes, which according to our view, if they do not exactly prove the centroepigenetic hypothesis, yet make it most probable, we now pass to the following chapter, which will afford as stated still another proof, even though a quite indirect one, for this hypothesis. For in showing that while a whole series of facts compels us to reject simple epigenesis, and a whole series of other phenomena compels us to reject preformation, it will make it seem very probable that a hypothesis which is able to bring both series of phenomena into accord must come close to the truth.

CHAPTER FOUR

PHENOMENA WHICH REFUTE SIMPLE EPIGENESIS; AND PHENOMENA WHICH REFUTE PREFORMATION. INADMISSABILITY OF A HOMOGENEOUS GERM SUBSTANCE; AND INADMISSABILITY OF PREFORMISTIC GERMS.

1. *Phenomena Which Refute Simple Epigenesis*

Roux designates, with the expression "self-differentiation" of a certain part of the organism, the process in which, according to a certain hypothesis, "the cause of whatever is specific in the differentiation of that part lies within this latter." And he calls "dependent or correlative differentiation" the opposite process, in which, according to other hypotheses, whatever is specific in the alteration which goes on in a certain part of the organism during development is determined by causes lying outside this part.[69]

If an ontogeny consisted only of self-differentiations, we should designate the development as evolutionary. If on the contrary, an ontogeny were produced only through dependent differentiations, we should call that a process of epigenetic nature.

[69]Wilhelm Roux: Die Methoden zur Hervorbringung halber Froschembryonen und zum Nachweis der Beziehung der ersten Furchungsebene des Froscheies zur Medianebene des Embryo. Anat. Anzeiger, Bd. IX. February 1894, P. 277—278. Gesamm. Abhandl., II, P. 978.

We note that theoretically a mixed or intermediate hypothesis would be conceivable, according to which a given part of the organism would be differentiated through the cooperation of causes lying within and without it. In case however the causes lying at any moment of ontogeny within the part concerned, do not arise through any antecedent process of epigenetic nature, the development at least up to this time must be considered as essentially purely evolutionary. But if, on the contrary, the internal causes do arise through an antecedent process of epigenetic nature the whole development would then be essentially of that nature.

Whitman states that the conception of modern evolutionists differs essentially from that of the earlier ovists and spermatists; for they excluded the formation of new structural parts during development, a thing which is naturally admitted by the evolutionists of to-day. According to Mivart's definition which Whitman accepts completely, "the term evolution may be employed, as it has been, to denote that the successive formation of parts previously not existent is due not to their imposition from without but to their generation from within." [70]

According to this definition which is essentially identical with that of Roux above cited, evolution, it may here be repeated, limits to a minimum the influence which the various other parts of the organism exert upon the development of each part, or considers it as absolutely non-existent, since each part contains within itself, or in any event in its immediate neighborhood, the causes of its progressive development. According to the epigenetic

[70] Whitman: Evolution and Epigenesis. Biol. Lect. at the Mar. Biol. Lab. of Woods Holl, Summer Session 1894. Boston, U. S. A., Ginn, 1896. P. 224.

hypothesis, this influence is, on the contrary, of the very greatest importance and is considered to be the only cause of each development.

We also can accept Mivart's definition in this sense. We note that it does not include in any way the conception of preformistic germs; for it is possible that the internal causes involved arise gradually in the course of development and need not be already present in the germ substance. In the first case, one has evolution without preformistic germs; in the latter, evolution with preformistic germs, which we would call preformation proper. This preformation proper, for example Weismann's type, is also included in the definition of evolution just given; it forms however only a special case of it, which is limited and approximates more the conception of preformation which the ovists and spermatists entertained.

The processes of epigenetic nature can be regarded likewise as belonging to two kinds, corresponding to the above mentioned categories of evolution. For one can conceive of processes of epigenetic nature both with preformistic germs and without preformistic germs, and both cases are actually met with.

In the first case the causes which bring about each specificity of development would be already present in the germinal substance. Only their liberation or activation in opportune time and place depends upon the reciprocal action of the different parts of the organism upon one another (for example DeVries, Oscar Hertwig, etc.). In the second, on the contrary, the causes producing the different specificities of development arise only gradually in the course of ontogeny, and always in con-

sequence of the reciprocal action of the different parts of the organism upon one another.

We will call the first of these processes epigenesis with preformistic germs, the other, epigenesis without preformistic germs, or epigenesis proper.

Further, each of these two processes can, theoretically, be divided again into the two following categories.

One can conceive of the reciprocal action of the different parts of the organism upon one another, as such that no part whatever should ever be considered different in any way, in so far as its formative action on the other parts is concerned, from these other parts, but rather all are to be regarded as equally necessary and of equal value in this respect. Or, on the other hand one can suppose that among all the parts there is one whose action upon the other parts differs through some peculiarity from the corresponding action of all other parts, so that it acquires in comparison with the latter much greater importance.

We shall designate the first process with the name "simple epigenesis," or briefly "epigenesis," which would be equally possible either with or without preformistic germs, and we shall call the second in which the formative action would on the contrary become specially localized in a definite zone of the organism, by the name of "localized or centralized epigenesis," or briefly "centro-epigenesis." Practically it would be conceivable only without preformistic germs.

Finally, in all the different theories without preformistic germs, one could conceive of the germinal substance as formed of a single homogeneous substance (or a homogeneous mixture of different chemical substances), or of a material which though not consisting of pre-

formistic germs, would nevertheless be formed of a greater or less number of specific parts different from one another.

Of all these hypotheses which one can form concerning the nature of the developmental process and the structure of the germinal substance, we need discuss here only the following chief ones, and consider these only very briefly, mentioning the others only casually in passing. We arrange them in the following way:

Concerning the nature of the developmental process:

1. Simple epigenesis with preformistic germs or without such.

2. Evolution with preformistic germs, i. e., preformation proper.

Concerning the structure of the germinal substance:

1. Germinal substance consisting of homogeneous material.

2. Germinal substance consisting of heterogeneous material. Here belongs the special case in which this substance consists of preformistic germs.

We can now pass on without further comment to a rapid review of the most important phenomena, on account of which simple epigenesis with preformistic germs or without such, cannot be admitted. This will oblige us sometimes to return to the phenomena and arguments with which we were occupied in the preceding chapter.

With the chief facts which are opposed to simple epigenesis we must now range the production, already mentioned and discussed, of right and left, anterior and posterior, half embryos of frogs, which resulted from the killing by a hot needle of one of the two first

blastomeres. As is well known it was these very half embryos that caused Roux to construct his evolutionistic theory, in which he compares development, at least in so far as the four quarters of the embryo come into consideration, with a mosaic work.

So long as the half formations arising from isolated blastomeres are limited to the very first divisions, so long for instance as one of the first two blastomeres, when isolated, limits itself to giving half of the total number of micromeres, or so long as the first cleavage spheres arising from the isolated blastomeres succeed each other and arrange themselves as if the two blastomeres had remained united, so long there is still nothing to be seen in these phenomena which would afford any proof against simple epigenesis. For in general we can suppose that the deutoplasm alone is the immediate cause of the number, and of the different relative sizes and disposition of the first blastomeres. If then the relations to the yolk of the blastomere and of the whole of the blastomeric group, could not by themselves constitute any proof change through the isolation of the blastomere, it is clear that the first cleavages must proceed exactly as though no isolation whatever had taken place.

So for example the isolated blastomeres of the two or four cell stage of the egg of the gastropod, Ilyanassa obsoleta, which divide in essentially the same manner as they would if they were part of the complete blastomeric group, could not by themselves constitute any proof whatever for or against any given developmental theory, so long as the separated blastomeric group does not take on any really specific form. For in this Ilyanassa obsoleta the yolk is distinguished by its great mass, thickness and

density.[71] And these peculiarities make it certain that the relation of the isolated blastomere to the yolk plasm is not different from that which would have existed had it remained united to the other blastomere.

But the preponderance of the determinative action of the yolk is limited usually to the early stages preceding the gastrula. It has no influence whatever on the final form of the embryo, no more than has for example, the temporary compression of the blastomeres between two plates or the shuffling of them. Therefore the early cleavage stages have no specific morphological significance, as is evident also from the above mentioned fact, that different related species and even quite widely separated species can present almost identical cleavage systems.[72]

It follows from this that as soon as development commences to take on its really specific form, that indicates that the action of the germ substance is preponderating over the action of the yolkplasm no matter in what way the latter may formerly have acted.

Consequently simple epigenesis certainly cannot have recourse, in order to explain the half embryos of Roux, to the fact that the deutoplasm remained unchanged in the unsegmented blastomere. For these half embryos arise at very advanced stages of development and represent quite specific formations.

Nevertheless Driesch seems to want to explain the half-formations in this way: "Each particle of the sur-

[71]H. E. Crampton, Jr.: Experimental Studies on Gasteropod Development. Arch. f. Entwicklungsmech. d. Organismen. Bd. 3; Heft. 1. Leipzig, Engelmann, March 24, 1896.

[72]Cf. E. B. Wilson: The Cell-lineage of Nereis. Journ. of Morph., Vol. VI, No. 3. Boston, U. S. A., Ginn, July 1892. P. 455.

viving half preserves as is shown by Roux's figures, the position which it would have had in normal development. Then after segmentation has taken place, the same formative factors act on each particle and on each blastomere respectively, which would have acted upon them in normal development, consequently also the same forms result; Ergo: half-embryo." [73]

From the epigenetic standpoint this explanation is inadmissible. For when the half embryo begins to take on the characteristic form of its species, and thereby indicates as we have seen that the specific action of the germ substance has from that time become preponderant over that of the deutoplasm, one could not assert that the same organ forming factors continue their action, for that would be to deny that there is any formative action at all exerted by the idioplasmic nuclear substance of one entire half, left or right, anterior or posterior, upon the other, developing half. This would be exactly the opposite of what simple epigenesis postulates, for it attributes the tendency of development to take on its specific form of equilibrium to the reciprocal action of all the innumerable little masses of one and the same idioplasm, which are active at the same time in all the nuclei of the entire organism.

Roux then can rightfully assert that the half embryos constitute by themselves the most direct and decisive refutation of the theory of epigenesis.

If we pass on now from half embryos to the regeneration of amputated organs, we know that this constitutes one of the most important arguments that the epigenesists ordinarily advance against preformation.

[73]Driesch: Analytische Theorie der organischen Entwicklung. Leipiz, Engelmann, 1894. P. 15—16.

But the preformationists on their side cite certain particular cases of regeneration as unfavorable to epigenesis: "Regeneration" remarks Roux, "takes place in tritons when all four extremities are removed at one time, from which it follows that for the formation of new extremities in one antimere, the presence of the other extremities is not in the least necessary, so that for this formation it is not necessary that there be any formative correlating influence extended from them." [74]

The anachronisms of development in which, for instance, certain parts remain behind other parts in their formation, or in which the germ layers may even develop with uneven speed, or one entire half of the body may take a jump ahead of the other half so that one can sometimes observe two different degrees of development in the two halves of the same embryo, belong likewise to the number of phenomena which simple epigenesis is incapable of explaining: "How the (epigenetic) conceptions of O. Hertwig," Roux writes further,—and his words, already quoted above, deserve to be repeated here, —"can be reconciled with these anachronisms in the development of the germ layers which I have observed, or indeed with the absence of the lower layer—the endoblast (Anentoblastia), while both of the other two layers remain essentially normal in the disposition of their parts, or finally with the formation of half embryos, may well be left to the reader's own judgment. For if such large parts can remain behind in their development, or indeed be lacking altogether, and the other parts be in no wise disturbed thereby in their development, it surely follows that the development of these latter is not con-

[74] Wilhelm Roux: Uber Mosaikarbeit etc. Anat. Hefte, Febr. 1893, P. 299. Gesamm. Abhand. II, P. 839.

nected by reciprocal actions with the absent parts, and therefore is not carried on by the reciprocal action of all the parts of the whole, one upon another." [75]

It is the same with headless monsters as with all monsters which lack entire parts of the organism but are nevertheless normal in the other parts. Because they show likewise that there does not exist any formative action exercised by the head, or by other parts, upon the rest of the organism.

While thus the head can be absent in development, the presence of certain other parts seems on the contrary to be indispensable in headless omphalosite monsters: "When one studies," writes Dareste, "headless, omphalosite monsters comparatively, one notes that the trunk is almost complete in some cases but in others incomplete. And upon this fact is based Isadore Geoffroy Saint Hilaire's division of headless monsters into three different types: the true acephali, in which the thoracic region is as well developed as the abdominal region; the paracephali, which have only the abdominal region; and the mylacephali in which only the sacral region is present. These three types arise through inequalities in the development of the cerebro-spinal axis. But how is it that the posterior part of this axis is always present, while the anterior part is lacking to a greater or less extent? Why does not the reverse appear in other cases? This depends evidently on some as yet unknown fact of embryogeny. For the present we must be content with the mere question." [76]

[75] Wilhelm Roux: Uber Mosaikarbeit etc. Anat. Hefte, P. 320. Gesamm. Abhandl. II. P. 859.

[76] Dareste: Recherches sur la production artificielle des monstruosités. Paris, Reinwald, 1891. P. 495.

Nevertheless some other varieties of omphalosite monsters seem to show that the presence of any part whatever of the vertebral axis is sufficient to permit at least partial development; for instance in the cephalic monsters the embryo consists generally of the head alone.[77] We note however that these monsters commonly contain the anterior extremity of the spinal cord which can have been only slightly differentiated in the embryonic stage at which the incomplete development is arrested. In some of these cephalic omphalosite monsters, a large part of this anterior extremity of the spinal cord may even have undergone a process of reabsorption after the previous arrest of the partial development.

As we shall see soon Born succeeded in producing artificially a thing like these cephalic omaphalosite monsters by grafting upon a complete tadpole a piece removed from another tadpole, and consisting only of the head and a small part of the elongated medulla.

Concerning the double monsters with double symmetry, it will be worth while to repeat once more *in extenso* the following statement of Roux, even though we have reported it already, for the most part, in the preceding chapter:

"This additional fact speaks directly against the achievement of development of the individual through a general, reciprocal, formative cooperation of all parts to form a whole; namely that in the chief class of double monsters, and so in those double formations which correspond to the law which I formulated of the double symmetry of the anlagen of organs, the piece absent in a symmetrically similar way from each of the two

[77]Dareste: Recherches sur la prod. artif. des monstr. P. 498.

individuals may actually be any given piece whatever that is limited by a plane surface; and that in them the organs are nearly all present in their normal form up to the plane of reunion, just as if two symmetrical pieces had been cut away so as to leave two plane surfaces, from two twins, after they were fully developed and ready for birth, and the foetuses had then been united by the cut surfaces. This normal formation of defective organs up to any given plane of separation as, for example, the 8-shaped double cornea or double lens of the third eye common to both organisms, speaks likewise strongly in favor of a capacity of self-differentiation possessed even by parts of these organs, as the simultaneous development of two structures united so extensively, to form bodies of which each is self centered, indicates directly the absence of the action of general reciprocal influences, connecting them into one whole." [78]

We remark nevertheless in our turn that the evolutionistic theory does not in any way explain as Roux asserts, how the two organisms are limited by a plane surface which is perfectly symmetrical, rather than by any kind of irregular surface whatever. This theory merely shows that it is possible that the development of organs which differentiate themselves automatically, may be arrested at any given surface, without thereby disturbing the normal form of any of the remaining portions, not even in the neighborhood of the surface where development is arrested. But it does not explain why the surface of division must be a plane surface, and perfectly symmetrical in the two individuals. One should rather expect here a manifold reciprocal inter-

[78]Wilhelm Roux: Uber Mosaikarbeit etc. Anat. Hefte, P. 320. Gesamm. Abhandl. II. P. 859—860.

locking of the two organisms which would give a most asymmetrical and irregular dividing surface.

The continuation of development in the tail fragment of the tadpole seems to speak likewise against both epigenesis and preformation. For in his experiments upon tadpoles, Born has proven the accuracy of Vulpian's statement that the amputated tails not only continue to live for sometime (some even thirteen days), but continue to grow and to differentiate into their various tissues. He has further observed the following processes of new formation.

"A few days after the amputation, the margins of the fin of the amputated tail commence to grow over the cut surface of the axis; they unite in front of it to form a high semicircular tail fin. The axis is not entirely without participation in this process, for prolongations of the notochord as well as of the spinal cord grow into the newly formed fin, but the metameric musculature shows nothing like this and terminates sharply at the original surface of amputation. But this prolongation of the notochord, like that of the spinal cord, even in the most favorable instances, scarcely extends half as far forward in front of the cut end of the original axis as does the newly formed marginal fin. This latter is formed of typical embryonic mucous connective tissue with a few pigment cells scattered through it. I have not been able to discover in it any rudiments of vessels."

"This observation teaches then," continues Born, "that the provision of yolk in the tail end cut off from a tadpole does not serve merely, as Vulpian has already shown, for further growth, and further differentiation of the tissues, and for the formation of a new structure growing out from the cut surface, but it shows that

besides the fin margin, the notochord and the spinal cord take part in this new formation. It is interesting that the tail of a tadpole is capable of such a regenerative new formation not only in the caudal direction but also in the opposite direction." [79]

We say then that these phenomena, which the amputated tail of the tadpole presents, can be cited by the preformationists against the epigenesists, as well as by the latter against the former. For the former can object that the progress of the histological differentiation in the fragment of tail cut off from all the rest of the organism would denote the absence of any action of the organism upon the development of this part of the body, and the epigenesists on their side could show that the power of the tail to regenerate even in the direction from the tail toward the head, could not be explained by preformation, even with the aid of reserve idioplasm, for that could effect regeneration only in the direction from the head toward the tail.

It is the same with Born's celebrated experiments on the grafting of certain fragments of tadpoles upon one another or upon complete tadpoles, which are opposed to simple epigenesis and at the same time indicate a process of epigenetic nature.

In the first place they are opposed to epigenesis. For in all grafts of parts of tadpoles upon complete tadpoles, the grafted parts have continued their development regularly as if they had remained united to their own organisms. Therefore the rest of this organism has not under normal conditions any influence upon the development of these portions.

[79]Born: Uber Verwachsungsversuche mit Amphibienlarven. Leipzig, Engelmann, 1897. P. 32—33.

Thus for example a larva of Rana esculenta from which there had been cut off the most anterior part of the head including the eye anlagen, the anterior part of the brain, the nasal groove, and the primitive mouth, was so grafted upon the caudal half of the abdomen of a complete larva, as to form an acute angle between the back of the former and the abdomen of the latter, the abdomen of the former being turned toward the head of the latter. After allowing the double larva twelve days of development, it was killed and it showed that "all the organs of the partial larva up to the surface of amputation and union had developed quite as completely as though there was no part of them lacking and as though their normal environment and their ordinary relations were quite undisturbed." [80]

The anterior portion of a larva so short that it scarcely extended beyond the commencement of the elongated spinal cord, was grafted upon the abdomen of a complete larva, and continued to develop normally. "All parts developed completely up to the surface of amputation: the cartilaginous trabeculae, the quadrates with the chewing muscles covering them, behind the mouth cavity the cartilages of Meckel, the cartilages of the lower jaw and behind these again the hyoids." [81]

Upon these and other similar examples, Born bases the following conclusions: "Although up to the moment of grafting there had been no trace (of primordial cranium) present, and the mesoderm from which it develops remained in a quite indifferent and almost primitive con-

[80]Born: Uber Verwachsungsversuche mit Amphibienlarven. P. 97.

[81]Born: Uber Verwachsungsversuche mit Amphibienlarven. P. 108—109.

dition, nevertheless the complicated and characteristic parts of the head were developed up to the surface of amputation completely and in their perfect form, and not only entire structure but also parts of these structures."

"Whatever development there is going on beyond the stage at which amputation was performed depends essentially on self-differentiation of the individual parts; no correlative influence of the neighboring parts or of the entire organism can ever be recognized, either negatively or positively. Thus this development beyond the stage at which amputation was performed, corresponds entirely with Roux's mosaic theory." [82]

Nevertheless, we shall see soon that another whole series of Born's experiments, as also those just recorded if one considers them from another point of view, are no less opposed to evolutionary hypotheses in general and to hypotheses of preformation properly so called in particular.

In short, the observations and experiments which we have thus far cited, from the half-embryos of Roux to the tadpole fragments of Born, all show the possibility that individual parts of the organism, provided they contain any part whatever of the vertebral axis, can develop independently of the remaining parts, and are sufficient by themselves alone to prove the inadmissibility of simple epigenesis.

But the preformists had yet another fundamental objection to make to the epigenesists, who have sought so far in vain for a reply to it: namely that epigenesis requires the renunciation of nuclear somatization. For these two hypotheses are absolutely irreconcilable. It

[82] Born: Uber Verwachsungsversuche mit Amphibienlarven. P. 204—205.

follows therefore that each fact or each argument which speaks in favor of nuclear somatization, is at the same time a proof against epigenesis. And we saw precisely in the preceding chapter, that there is a whole series of facts and arguments, which it would be useless to repeat here, but which compel us to admit this nuclear somatization as an incontrovertible fact.

The preformationists can finally object to epigenesis and not unreasonably, that by its "attainment of equilibrium," it does not explain the termination of ontogeny as well as preformation does. For why should the reciprocal actions of all parts, on which development depended up to that time, suddenly cease to effect any further change when once the adult stage is reached? Because it is only then, reply the epigenesists, that the dynamic equilibrium is attained. But if the successive ontogenetic forms repeat the phylogenetic, how comes it that the dynamic equilibrium which once existed in each of these latter does not remain existent in any of the former? And if the absence of equilibrium at all these stages is due to some alteration of the formative living substance, how then could this new substance pass again during a long series of stages through the same phylogenetic ancestral forms? The preformists, on the contrary, have no trouble in explaining the arrest of development since according to their theory it would follow only at the moment when there would be present in each cell only a single kind of preformistic or determinant germs.

Having thus made a rapid review of the principal objections which compel us to reject epigenesis, we can pass on to an equally brief consideration of a number

of objections which stand in the way of admitting preformation.

2. *Facts Which Compel the Rejection of Preformation*

If, limiting ourselves to the most typical theory of preformation to which all the others can be finally reduced, we consider that of Weismann, we encounter at the outset a very simple argument which is yet so formidable that it is in itself enough to discourage the most firmly convinced partisan of that doctrine.

For the preformation theory of Weismann forces him to suppose for the infinitely numerous particles constituting the different determinants or groups of determinants, an excessively complicated architecture or excessively complicated arbitrary mode of disposition. Now the elementary fact of reproduction demonstrates that the constitution of the germ plasm, whatever it may be, does not become at all altered when this latter divides and distributes itself among the incalculable number of germ cells which can be produced by each organism and by all its succeeding generations. Weismann must first then explain to us how the subdivision of a given germ plasm into new parts in each of which this very complicated structure is preserved uninjured or is accurately reproduced again, is possible. That is fundamentally the same difficulty which the old ovists and spermatists encountered, and which they endeavored to overcome by their idea of the encasement of the germs.[83]

Weismann has since endeavored to weaken the force

[83]Among others compare e. g. Oscar Hertwig: Präformation oder Epigenese? P. 11.

of this objection by taking into consideration, besides the architecture of the germ plasm itself, also the uneven rapidity of multiplication of the different determinants and the reciprocal forces of attraction exercised by these latter upon one another, as factors which determine the orderly division of each plasm or each id.[84] But, as this author himself admits, the architecture of the germ plasm remains necessarily the principal factor, and consequently the objection of the incompatibility of this arbitrary architecture with constant complete division of the plasm without alteration, remains in all its force.

Another argument which presents itself likewise against preformation is, that with the exception of the partial developments cited in the preceding section of parts which each contained one very definite zone of the organism, it has never been possible to obtain the development or the continuation of development of somatic parts, even though they are capable of living for some time after they have been detached from the rest of the organism.

One would certainly not regard as a continuation of normal development the mere increase in mass which takes place in parts cut off from the fetal organism, when they are transplanted upon tissues which on account of their great richness in blood vessels are especially capable of affording abundant nourishment to their new guests.

This simple increase in mass depends for the most part on an actual multiplication of the respective cells, which proceeds in directions determined either by nutrition alone or by the path of least resistance in the environ-

[84]Weismann: Das Keimplasma. Eine Theorie der Vererbung. Jena, Fischer, 1892. P. 86.

ment, accompanied either by no morphologic alterations or by quite aspecific ones, depending upon whether the portion cut away consisted of a formless fragment of tissue, or of an organ whose proper form was already indicated. We may mention, for example, Zahn's transplantations of portions of cartilaginous or bony fetal tissues to the lungs and kidneys of other individuals of the same or different species,[85] or Fischer's transplantations of anterior and posterior extremities of chicken embryos (especially of one incubated only eleven days) to the comb or ruff of the cock.[86]

It is true that both, and especially Fischer, have observed that in these extremities of chicken embryos, ossification, which at the time of amputation had not commenced at all or had scarcely commenced, was initiated or continued in the transplanted extremities.[87] But this process of ossification can be considered only as the mere accumulation, and consequent intensification, of the effects of the specific vital activity which was already at work before the amputation, and which persists unaltered after the transplantation.

Consequently we think that Roux is quite wrong when, apropos of these experiments of Zahn, Fischer, and others, he expresses himself as follows: "These experiments have demonstrated that many isolated embryonic parts can not only grow but even become

[85]Zahn: Uber das Schicksal der in den Organismus implantierten Gewebe. Virchows Archiv, Bd. 95. Drittes Heft, 5. March 1884; especially e. g. P. 374—375, 380, 381.

[86]Fischer: Uber Transplantationen von organischem Material. Deutsche Zeitschrift der Chirurgie, Bd. 17. Erstes, Zw., Dr. u. Viertes Heft, 1882; especially e. g. P. 362—363, 370—371.

[87]E. g. Zahn: Uber das Schicksal etc. P. 382ff.—Fischer: Uber Transplantationen etc. P. 370, 374.

histologically differentiated in an approximately normal way. It follows that the differentiation of these parts is not a function of reciprocal actions between these parts and other parts. Therefore there is thus already proven a certain histologic and morphologic self-differentiation of many parts of the developing egg." [88]

This is not correct. For these experiments show, we repeat, only a mere increase in mass of these tissues, which is morphologically without any specific character; and the continuation of the histologic differentiation which had already commenced or was on the point of commencing at the moment of amputation, is explicable by the simple accumulation of the effects of the same vital process which merely persists exactly as it was before the amputation.

Another argument against preformation is the great capacity of modification of the organism while it is undergoing development, as well as when fully developed, to which it owes its remarkable power of adapting itself to quite abnormal conditions. For the preformation theory with its determinants, which are bound up with one another into a solid structure, and of which each determines the formation even of the smallest particles and their most minute variations, implies undeniably a great morphological rigidity, which is not reconcilable with the great mutability of the organism.

"Galls," says Oscar Hertwig, for example, "are valuable witnesses against the germ theory of Weismann. They teach us that cells of plant bodies can serve quite other purposes than could have been foreseen during

[88] Wilhelm Roux: Zur Orientierung über einige Probleme der embryonalen Entwicklung. Zeitschrift für Biologie; Bd. XXI. July 1885. P. 480—482. Gesammelte Abhandlungen. II, P. 206—207.

development, that they can adapt their form to new conditions, and that their specific form is not determined by special determinants in the nucleus but by external stimuli." [89]

The stomach of the tern, which ordinarily feeds on fish, is lined by a soft mucous membrane. If one feeds it with wheat for a few weeks its stomach develops a superficial horny coat, its musculature is strengthened and it takes on the character of a gizzard.[90] If these stomachs belonged to two varieties of the same species, Weismann would have no hesitation in attributing the diversity to special, and thus different, determinants which, as the facts show, do not really exist.

Loeb has demonstrated that the colored design of the yolk sac of a fish embryo (Fundulus) is not in itself predetermined, but depends upon the distribution of blood vessels. The pigment cells are at first distributed uniformly but when the circulation of the yolk sac is established, they migrate toward the vessels, attracted probably, as Loeb supposes, by a chemical substance in the blood, and give rise thus to a definite design. Graf has likewise recently demonstrated that the color designs of the leech are not themselves inherited, but that they depend upon the disposition of muscle fibers in which the amoeboid pigment cells lie. It would be absurd, concludes Wilson, to imagine in all of these cases a special series of determinants for each individual color design.[91]

[89]Oscar Hertwig: Zeit- und Streitfragen der Biologie. I. Präformation oder Epigenese? P. 48—49.

[90]Delage: L'hérédité etc. P. 604.

[91]E. B. Wilson: The embryological Criterion of Homology. Biol. Lect. at the Mar. Biol. Lab. of Wood's Holl; Summer Session 1894. Boston, U. S. A., Ginn. 1896. P. 116.

Everybody knows the peculiar static structure of bone. Substance becomes accumulated in bone at the points of greatest pressure, and attains thus its best possible utilization. Now it is known, as J. Wolff discovered and as Kastor, Martiny and J. Rabe have confirmed, that similar structures are formed also in quite new and abnormal circumstances in connection with new static conditions, for example, in bones broken and reset at an angle. "From this it follows," says Roux, "that these formations do not need to be fixed and inherited, but arise of themselves whenever the conditions exist. As the static structure of bones is developed in a clearly recognizable form only after the first years of life, one can not say anything of the necessarily hereditary transmission of it, without special researches upon this point." [92]

Teratogenesis in general, both natural and artificial, is quite opposed to preformation. It denotes that the organism, at any rate while it is still in process of development, can adapt itself to exceptional conditions which are quite different from the normal. And it accomplishes this by producing abnormal formations whose development must consequently be due only to a process of epigenetic nature, and cannot be of preformistic nature.

Let us consider one of the simplest examples. In the hemiteratic spina bifida, the spinal opening is ordinarily covered over by a layer consisting of fibrous tissue like that of scars, which in some cases takes on all the characters of the skin. Then the spinal opening is not visible from the outside. But when the spinal opening is in the lumbar region it is not rare for a

[92]Roux: Der Kampf der Teile im Organismus. P. 28.

considerably developed tuft of hair to appear on the outside.[93] Would Weismann also presuppose its own determinants for this tuft? And if this tuft arises without being represented in the germ plasm by its own determinants, why cannot the same process occur in normal development for other parts of the organism? Normal and abnormal development do not differ essentially from each other; and the causes which produce them are of the same nature in both.

Weismann certainly recognized the great importance of the capacity of alteration by functional adaptation, possessed by both embryonic and adult organisms. "If this principle did not exist," he writes, "the organism would be like a building, of which each stone is already prepared before the situation and use of the building is determined. Such a predetermined ontogenesis could not produce any organism capable of living. The influences under which organisms exist during their development are never exactly the same and to be able to adapt themselves to them they must possess a certain freedom." [94]

But we cannot repeat often enough, that this great capacity of adaptation is absolutely irreconcilable with his theory of determinants, or with any preformistic composition of the germ substance. If functional adaptation effects "the adjustment of the primary hereditary anlagen, that is of the determinants, to new circumstances," [95] this signifies that these new circumstances

[93]Dareste: Recherches sur la production artificielle des monstruosités. P. 327, 538.

[94]Weismann: The Effect of External Influences upon Development. The Romanes Lectures, 1894. P. 16—17.

[95]Weismann: Ibid, P. 16.

external or internal to the individual exert upon these determinants a certain formative action. But if one assumes that a certain formative action becomes thus exerted upon each of the determinants by abnormal circumstances in their development, one must then assume that a similar formative action is exerted upon each of these same determinants by the other parts of the organism when the development of these parts proceeds quite normally. But what remains then of the preformistic action of these determinants which should fashion the organism like a piece of mosaic-work?

The experiments of Born also, which, as we have seen above, are absolutely opposed to simple epigenesis are just as little reconcilable with preformation, because they denote in general the epigenetic nature of the process of growth. We need recall here only the union of portions of different tadpoles; for example, of the anterior portion of one tadpole with the posterior portion of another.

In this latter case, if the anterior portion were limited by a section passing through the medulla oblongata, while the posterior portion had been obtained by a section passing through the medulla spinalis, it would follow that the two surfaces of amputation of the medulla which ought to match exactly would present on the contrary unlike forms and surfaces. In spite of this a short time after the two ends of the medulla were united, the two half tadpoles having meanwhile continued their development, they showed a union in which no angle or sharp fault persisted but gentle curves of transition were present instead. The two medullary canals went over into one another also gradually and without interruption, so that one could no longer recognize the exact

point of their union. "This is an example of the phenomenon observed also in all the other organs, that after the growing together of two sections of unequal size and form, the uneven character of the union, present at first, disappears and gradually a smooth connection of the surfaces is established." [96]

The union of the corresponding organs of the two fragments is quite intimate: for example in the case which we have just cited, longitudinal sections of the two united medullas showed that the fibers of the white substance of the medulla spinalis went over continuously into those of the white substance of the elongated medulla oblongata.[97]

Among the experiments of Born, those upon the artificial production of double monsters are especially remarkable. They were obtained by joining two tadpoles together in the most diverse ways. In the case which we now report he cut away from each of two tadpoles the upper part of the ventricles of the brain and joined the two cut surfaces together so that both the tails and the bellies of the two tadpoles constituting the double monster were directed in opposite ways. Here also, there took place, in so far as the two tadpoles developed, a complete union so that after sometime there could not be perceived any transition stage between the surfaces of the corresponding organs which were united together.

"It is impossible to believe," remarks Born in this connection, "that in placing these two tadpoles one upon the other, the small ventricular clefts and the external walls of the two brains could be applied exactly one upon

[96]G. Born: Uber Verwachsungsversuche mit Amphibienlarven. P. 53—54.

[97]G. Born: Uber Verwachsungsversuche usw. P. 56.

another." In such cases, which are repeated over and over, there is no escape from the admission that with the progress of growth there has taken place in the blended organs a sort of smoothing out, "Ausglättung," of the external and internal walls, and perhaps even a transitory modification of the normal form, caused simply by the influence of the similar organs growing together.[98]

In other cases there is more than a simple smoothing out of the two surfaces which would not fit together at first. Thus in the union of two parts of the intestine of double monsters, thoracopagi, gastropagi, and ventropagi, obtained by cutting off from each of two tadpoles a thin layer of the abdomen, and superimposing the two cut surfaces as usual, there results an exact conjunction of the two thin-walled intestinal tubes in such a manner as to constitute a single tube without any trace of the junction which was made. So exact a coaptation can certainly not be effected by the simple superposition of the two tadpoles.[99]

Sometimes the corresponding organs of the two larvae seem as though seeking each other and reaching out to each other. They both deviate from their ordinary direction in order to be able to unite and extend one into the other. This phenomenon appears characteristically in the fusion of the two vascular systems as is demonstrated in the clearest manner by certain experiments in grafting definite portions of tadpoles upon complete tadpoles: as for example, the grafting of the posterior heartless portion of a tadpole upon the abdomen of another complete tadpole: the fusion of the two vascular systems is so complete that a single blood circulation

[98]G. Born: Ibid. P. 141.
[99]G. Born: Ibid. P. 69—86.

is produced, the heart of the complete tadpole putting in circulation the blood of the grafted portion also.[100]

This phenomenon is presented also very strikingly in the mutual prolongation one into another of the pronephric and other secretory ducts. Thus in a double monster obtained by uniting the anterior portions of two tadpoles, the left pronephric ducts met and grew together although at first their extremely fine cut ends certainly lay some distance apart and their directions crossed almost at right angles.[101]

All these phenomena are hard to reconcile with the rigidity implied in Weismann's determinants. They speak on the contrary entirely in favor of a general process of growth that is epigenetic in nature; for only to a process of growth of this nature can be ascribed all the phenomena of adaptation and of deviation from the normal form which result in the complete and exact conjunction of the various corresponding portions of different individuals.

Against the rigid preformation of Weismann, which attributes development exclusively to qualitative nuclear divisions, Roux himself furnishes a most appropriate argument which even the most pronounced anti-preformists rarely cite.

"In the larger animals of the same species the cells are not correspondingly larger than in individuals which in consequence of lack of nourishment have remained smaller. Thus the unequal size of the individuals must be associated with an unequal number of cell divisions, which by the method of qualitative differentiation assumed by Weismann must lead to a very essential

[100]G. Born: Ibid. P. 87—88.
[101]G. Born: Ibid. P. 144.

disturbance. It follows that qualitative differentiation can not have any close association with the number of cell divisions, nor indeed with the process of cell division itself, so that it is not possible for any definite qualitative alteration to be so associated with each individual cell division as to produce a definite character in each somatic cell of the tenth, eleventh, twelfth, twentieth, and fiftieth generation from the egg cell in consequence of this number of generations." [102]

To circumvent this objection to the preformation theory, Roux has recourse to the hypothesis of a self regulating mechanism of frankly epigenetic nature which really amounts to reducing the part played by preformative processes in ontogeny to a wholly subordinate role.[103]

But the strongest objections against preformation are on the one hand the above mentioned experiments on isolation of blastomeres, and the production of double monsters from a single egg and other similar ones, and on the other hand the experiments upon regeneration.

The experiments upon the isolation of blastomeres which showed that each one could produce an entire individual are, as we have already explained in the preceding chapter, a convincing proof that at least the first nuclear divisions are not qualitatively unequal. Having recourse to a reserve idioplasm implies the renunciation of preformist theories. For in the first place, it really admits that the whole of the idioplasm (active

[102]Wilhelm Roux: Uber die Bestimmung der Hauptrichtungen des Froschembryo im Ei und über die erste Teilung des Froscheies. Sep.-Abdruck aus der Breslauer ärztlichen Zeitschrift, 1885, P. 35. Gesamm. Abhandl. II. P. 316—317.

[103]Wilhelm Roux: Ibid. P. 35, 317.

plus reserve idioplasm) remains after division just as it was before; in the second place, the conception by which one makes the activation or non-activation of the reserve idioplasm depend upon the abnormal or normal relations of the different nuclei with one another is very similar to that of epigenesis with preformistic germs, such as would correspond somewhat with the hypothesis of DeVries or that of Oscar Hertwig.

The formation of double monsters from a single egg constitutes essentially an analogous case to that of the formation of entire individuals from isolated blastomeres. We mention for example the experiments of Wilson in which following the simple displacement in relation to each other of the first two blastomeres of the egg of Amphioxus, each of those blastomeres produced a gastrula united along a more or less extensive surface with the gastrula produced by the other blastomere in such a manner as to give rise to numerous and very varied forms of double gastrulas in which the axes and respective blastopores of the twin gastrulas were oriented in the most diverse ways in relation to one another.[104] The same thing occurred in the similar double monsters obtained by Oscar Schultze from frogs' eggs, which were produced by compressing the egg between two horizontal plates and turning them over immediately after the first segmentation.[105]

If these double monsters,—and Roux has remarked

[104]E. B. Wilson: Amphioxus and the Mosaic-Theory of Development. Journ. of Morphology, vol. VIII, No. 3. Boston, U. S. A., Ginn. August 1893; P. 591—595. Table XXXIV.

[105]O. Schultze: Die künstliche Erzeugung von Doppelbildungen bei Froschlarven mit Hilfe abnormer Gravitationswirkung. Arch. f. Entwicklungsmech. d. Organismen Bd. I. Heft 2. Leipzig, Engelmann, 1894. P. 276—284. Tables XI and XII.

this himself, as we have seen in the case of those with double symmetry,—are opposed on one side to simple epigenesis because they show that between the two organisms, even though they have so great a part of the body in common there do not exist any general reciprocal actions tending to make a single whole of the two bodies, they are on the other side, also opposed to preformation, in that they demonstrate in the same manner as do the experiments upon isolation of blastomeres, the equipotency or qualitative identity of the two first segmentation nuclei.

And this equipotency is not limited only to the two first but exists also in all the first blastomeric nuclei as is demonstrated by the inverse phenomenon obtained by Morgan of the formation of a single embryo from two blastulas of Sphaerechinus which had grown together of themselves.[106]

Finally preformation as we have said, is quite irreconcilable with all the manifold processes of regeneration without exception.

Above all, Weismann interprets in fundamentally the same sense as we, the experiments and observations of Roux upon the peculiar regeneration constituted by the postgeneration or completion of the half embryos which we have so often mentioned. For they signify as he himself admits, "that this completion took place by a kind of cell infection, of such a nature that mere contiguity, for example with ectoderm cells, caused the as yet undifferentiated cells of the side operated upon to become developed into ectodermal cells, while similar contiguity with me-

[106]E. H. Morgan: The Formation of one Embryo from two Blastulae. Arch. f. Entwicklungsmech. d. Org., 1895. Bd. II. Heft 1. P. 65—71.

soblastic cells made them become mesoblastic cells." And Weismann finally calls into question the incontestability of these facts, just because such a cell determination dependent upon contiguity would upset at once his whole theory of preformation.[107]

But there are also many cases of regeneration proper in which one has a remodeling of old tissues into new tissues that are quite different, and they constitute phenomena which are analogous in this respect with post-generation. As an example may be mentioned the regeneration of Planaria maculata.

Fragments of this worm obtained by two transverse sections regenerate the head and the tail by producing new cells. But after their formation, this head and this tail do not grow any further, but the entire subsequent growth in length of the body takes place in the older more pigmented parts, so that the normal relative proportions of the planaria are restored simply by a remodeling of the older tissues. "The fragment of the worm reacquires its normal form but not through the addition of new tissue at the anterior and posterior extremities, except to a very small extent. The transformation is produced chiefly in the old tissue after the head and tail are developed. Thus we find here not only the capacity of regeneration but also a subsequent self-regulation by means of which the normal relations of the parts characteristic for the species become re-established." But that is not all. For in animals regenerated from lateral fragments, the longitudinal axis of the new worm is found often in the older tissue, so that one portion of the old material which was in the right side of the old animal becomes now part of the left

[107]Weismann: Das Keimplasma. P. 192.

side of the new animal or vice versa; and the development of the new pharynx which is found in the exact longitudinal axis, indicates that it can be produced indifferently from any part whatever of the old tissue.[108]

This remodeling of old tissues into new tissues differing from them indicates that the supposed determinants of Weismann have not by themselves any value, for as soon as the tissue finds itself in conditions different from the normal ones it takes on forms and acquires properties which would require determinants of quite another nature. "The organism," writes Whitman, "dominates cell formation using for the same purpose one, several, or many cells, massing its material and directing its movements and shaping its organs as if cells did not exist or as if they existed only in complete subordination, if I may so speak, to its will." [109] And one would not know how to give any better proof of the correctness of this statement than that which is constituted by these particular regenerations, which utilize the material already existing to remodel it into the new.

And not only are these phenomena of peculiar regeneration irreconcilable with preformation but the very fact of regeneration in general is irreconcilable with it.

"The germ tissue of the new organ," writes Hertwig, "does not contain any remnant of the amputated organ itself from which it could be reproduced by simple growth. The buds destined to reconstitute the eye-bear-

[108]E. M. Morgan: Experimental Studies on the Regeneration of Planaria maculata. Arch. f. Entwicklungsmech. d. Org. Bd. VII. Heft 2. and 3. Leipzig, Engelmann. Oct. 18, 1898. P. 385, 389, 395—396.

[109]Whitman: The Inadequacy of the Cell-Theory of Development. Biol. Lect. at the Mar. Biol. Lab. of Wood's Holl, Summer Session 1893. Boston, U. S. A., Ginn 1894. P. 119.

ing tentacles of the snail contain no trace whatever of retinal cells nor of pigment cells, nor of any other sensory cells whatever. Similarly the buds for the extremities do not contain any trace of the material of the carpus and phalanges nor of the muscles and tendons belonging to them. It is a complete new formation." [110]

The explanation which Weismann endeavors to give of these complete new formations produced in every regeneration is well known:

"If each cell of the completely developed bone contains within it only that kind of idioplasm which controls it and which is consequently the molecular expression of its own particular nature, it would be impossible to understand how the regeneration could be effected of a bone which had been, for instance, cut through longitudinally. Supposing that because of the wound there would become exercised upon the cells of the stump a stimulus which caused them to proliferate, a mass of bony tissue would indeed be produced but never a bone of definite size and shape. This can take place only in case the cells undergoing proliferation possess, besides their active determinants, an additional supply of determinants which control the missing part about to be reformed. It is then evident that, if we wish to transport the Nisus formativus of Blumenbach into the cell and indeed into its idioplasm, we must assume that each cell capable of regeneration contains besides its principal idioplasm, also an accessory idioplasm ('Neben-Idioplasm'), consisting of the determinants of the portion of the amputated organ which can be regenerated by it. Thus, for instance, the cells of the humerus must contain besides their own con-

[110]Oscar Hertwig: Die Zelle und die Gewebe. II. P. 180.

trolling determinants also all the determinants of the forearm and of the hand as accessory idioplasm, for they can cause the entire chain of these bones to be formed anew; and the cells of the radius must contain as accessory idioplasm all the determinants of the radial portion of the wrist, hand and fingers.

"We can regard this theoretical requirement as quite realizable also, since when the whole organ commences to be formed, the necessary accessory idioplasm can very well separate from the disintegrating embryonic idioplasm. We need only assume that this accessory idioplasm remains henceforth inactive in the nuclear substance of the cell until some cause for regeneration arises." [111]

We note at once that, according to this hypothesis, there is no reason at all why there should be held in reserve in each part of the bone only the accessory idioplasm capable of regenerating the bony parts distal to that point, but never any other capable of regenerating a larger or smaller part. Each particular reserve idioplasm, when once it has separated itself in a given cell from the principal idioplasm, and been segregated in the nucleus of the cell itself in the latent state, will be able to preserve itself unaltered through many generations of cells. Consequently there must be present at any point at which a bone may be broken several accessory idioplasms, each capable of regenerating a more or less long portion of the bone which was broken, and perhaps also of some other bone. In the illustrative case cited by Weismann the second phalanx should contain besides the reserve idioplasm capable of regenerating the second and third phalanx,

[111] Weismann: Das Keimplasma. P. 136—138.

also that which is capable of regenerating all three phalanges; or the distal part of the second phalanx should contain, besides the accessory idioplasm capable of regenerating the distal portions of the second phalanx and the whole of the third phalanx, also that which is capable of regenerating both the third phalanx and the entire second phalanx itself. Why, then, should only that accessory idioplasm become activated which is capable of regenerating just the particular part cut off?

Further, Weismann himself recognizes that when different tissues and organs are cut through, "it is only the harmonious equipment of the cells of a definite cross section with groups of determinants, different but mutually adaptable, in accord among themselves and complimentary, that could make regeneration of the higher type possible." [112] But really it is not easy to conceive how this harmonious equipment of reserve idioplasm could be guaranteed in the great number of different cells of a complex section.

Roux has seen so clearly this impossibility of explaining the phenomena of regeneration by preformation theories, that he asserts that in "direct" or "typical" generation self-differentiation may have the preponderance over differentiation due to reciprocal actions among the parts without nevertheless entirely excluding it; but in regeneration, which he calls "indirect" or "atypical" generation, he admits that differentiation of epigenetic nature must necessarily prevail over preformation.[113]

Weismann has rightly been unwilling to fall into the contradiction of imagining two different natures for two

[112]Weisann: Ibid. P. 297—298.

[113]Roux: Über Mosaikarbeit usw. Anat. Hefte. P. 279—331. Gesamm. Abhandl. II. P. 819—870.

processes which are essentially identical with each other, but has been thereby driven to an attempt at explanation, which is wholly artificial and indefensible.

In order to make the artificiality of his interpretation of the most difficult cases clearer, let us consider further the following examples.

It is known that regeneration is not usually an exact repetition of the ontogenetic process.

"Until the last few years," writes Delage, "it has been regarded as a dogma that regeneration is a repetition of ontogeny. That is that the regenerating organ or limb goes through the successive stages of development through which it went in its first formation. Yet the question has not been thoroughly enough investigated to permit the statement that it always does this, and in many cases it is certain that it does not proceed in this way. Thus a round tailed salamander regenerated a round tail from the first and not the flattened finlike tail of the larva, the crab regenerates an adult foot and not a foot like that of its larva, *Zoaea*. The limb or organ regenerated after a wound arrives at once at the stage which corresponds to the age at which regeneration takes place." [114]

Further, regenerations of ectodermic tissues at the expense of entodermal or mesodermal tissues are not rare. We have already seen how the crystalline lens, embryologically of ectodermic origin, regenerates in the triton from the mesodermic iris. The anterior intestine of Tubifex rivulorum, whose ontogenetic origin is ectodermal, regenerates, with the exception of a small portion at the end, from entodermal tissues.[115]

[114]Delage: L'hérédité etc. P. 104—105.

[115]H. Haase: Über Regenerationsvorgänge bei Tubifex rivulorum Lam. mit besonderer Berücksichtigung des Darmkanals und Ner-

Finally, cases are not rare in which a regenerating organ alters its form, as in the lizard in which the new tail has a skeleton not formed of individual vertebrae at all, but of a little continuous, cartilaginous cylinder.

Now the epigenetic theories explain very easily how it comes that the part amputated can follow in its regeneration a shorter road than in its ontogeny (caenogenetic regeneration), and how in many cases after completion of the process, it may have a form quite different from that of the original part. For the remaining part of the body, on which the morphologic determination of the amputated part depends, is now in the adult state while formerly it was in the embryonic state.

The altered condition in which it now exerts its formative action upon the part in process of regeneration explains the diversity, not only of the earlier results obtained, in which development and regeneration proceed in different ways, but also of the final results, in which the regenerated part is of abnormal conformation. For the differences of conformation which are produced at the commencement of the process of regeneration cannot always be smoothed out and effaced when, at the end of the regenerative process, the condition of the rest of the organism from which the formative action is exerted upon the part in process of regeneration becomes again the same in relation to that latter as at the end of normal ontogeny.

Weismann on the contrary, whose above quoted explanation is clearly no more adapted to these cases, is forced to take refuge in the following subsidiary hypothesis:

vensystems. Zeitscher. f. wissensch. Zoologie. Bd., 65. Zw. Heft, 1898. P. 229—235.

"In caenogenetic regeneration, (and *a fortiori* when the regenerated part remains of abnormal conformation), one cannot but admit that certain double or multiplied determinants must be present beside one another in the germ plasm, some of them being destined to embryonic development, others to regeneration. These latter must have their interior forces and particularly their growing force so arranged in advance as to split off, either alone or together with neighboring determinants of regeneration, as reserve idioplasm, at the proper moment of development." [116]

Epigenetic theories contain in themselves an immediate explanation of the well known fact that when a worm is cut in two, the anterior part regenerates the posterior while the posterior regenerates the anterior.

Weismann on the contrary is forced to have recourse to the following artificial hypothesis: "As the two halves become always complete again, no matter at what place the worm is cut, it therefore follows that the cells situated in any particular transverse planes of the body are not merely provided with reserve determinants for generating in some planes the head, in others the tail, but every cell must be able to act in either way, according to whether it happens to lie anteriorly or posteriorly to this plane. In order therefore to explain the twofold reaction of these cells, and stick to our fundamental view,—which regards the cells concerned in regeneration, as arranged and controlled by forces lying within themselves, and not by any external directing power,—it seems to me that we must assume that each of them contains two different reserve determinants, one for reconstruction of the head, the

[116]Weismann: Das Keimplasma. P. 145—146, 147.

other for that of the tail end, and that one or the other becomes active according as the stimulus due to lying uncovered, is applied to the anterior or posterior surface of the cell concerned." [117]

Finally according to epigenetic theories the regeneration of the hydra is a process which does not differ essentially from any other process of regeneration, but according to Weismann's theory the following complicated additional explanation becomes necessary.

"If one divides a hydra in a longitudinal plane the two halves grow again into entire individuals, irrespective of the plane of section. As a transverse section of the animal at any point which may be selected is followed likewise by the complete reconstruction of each of the two halves it follows that every part of the body of the hydra must be capable of regeneration in a threefold direction, namely in the three directions of space. As the body is differently constructed in these three directions we are forced to the conclusion that each of its cells must contain groups of determinants of three different kinds. * * * And it cannot be the quality, but the direction from which the stimulus of the wound comes to each cell, which will decide for it which of the three groups of determinants will become active." [118]

We believe that we do not pronounce too severe a judgment, if we affirm that so artificial a hypothesis demonstrates the absolute incompetency of preformation theories to explain the phenomena of regeneration.

What is the conclusion which can be drawn from all that we have said thus far in the present chapter?

[117]Weismann: Das Keimplasma. P. 169.
[118]Weismann: Das Keimplasma. P. 170.

The first part has shown us that simple epigenesis is directly and decidedly controverted by a whole series of indubitable facts and results which no one now opposes. The second part, which refutes preformation, shows us on the contrary that the nature of every process of development is really epigenetic.

And thus a correspondingly greater probability is established for those hypotheses which, concentrating the power of sending forth the controlling influences of development into a single well defined zone of the organism, thereby explain quite as well as epigenesis the facts that are irreconcilable with preformation, and are at the same time in accord also with all the facts which simple epigenesis is incapable of explaining.

3. *Inadmissibility of a Homogeneous Germinal Substance*

It will not be necessary to give this question more than a very brief consideration, for it is sufficient to mention the chief argument which all the partisans of preformistic germs, the epigenesists as well as the preformists proper, have repeated incessantly and still repeat. The fact that in doing this each uses almost the same expressions as the others shows how conclusive this argument is.

"The considerations," remarks Wilson, "which have led to the rehabilitation of the theory of pangenesis are based upon the facts of what Galton has called particulate inheritance. The phenomena of atavism, the characters of hybrids, the facts of spontaneous variation, all show that even the most minute characteristics may appear or disappear independently, may be modified inde-

pendently, may be inherited independently from either parent, without in any way disturbing the equilibrium of the organism, or showing any correlation with other variations. These facts, it is argued (by the partisans of preformation), compel us to believe that hereditary characters are represented in the idioplasm by distinct and definite germs (pangens, idioblasts, biophores, etc.), which may vary, appear or disappear, become active or latent, without affecting the general architecture of the substance of which they form a part. Under any other theory we must suppose variations to be caused by changes in the molecular composition of the idioplasm as a whole, and no writer has shown even in the most approximate manner how particulate inheritance can thus be conceived." [119]

It is well known that this is really the principal argument, one might say the only one, which Galton brings up in defense of his germs, substituted by him for the gemmules of Darwin: "The independent origin of the several parts of the body can be argued from the separate inheritance of their peculiarities. If a child has its father's eyes and its mother's mouth these two features must have had a separate origin. Now, it is observed that peculiarities even of a microscopic kind are transmissible by inheritance, therefore it may be concluded that the most minute parts of the body have separate origins." [120]

The argument which DeVries brings up in favor of his pangens, or material particles representative of the

[119]E. B. Wilson: The Mosaic Theory of Development. Biol. Lect. at the Mar. Biol. Lab. of Wood's Holl: Summer Session 1893. Boston, U. S. A., Ginn, 1894. P. 3—4.

[120]Francis Galton: A Theory of Heredity. Journ. of the Anthropological Institute. January 1876. P. 331.

different characters of the organism, is quite similar to that of Galton. It is summed up in the following passages from his book: "Many species of plants," writes he, "have the power of producing definite chemical compounds: among the most important of these are the red and blue coloring substances of flowers: also the various tannic acids, the alkaloids, the etherial oils, and numerous other products. A small number only of these compounds are limited to a single species of plants: a large number are present in two or more species, systematically far removed from one another. There is no reason to believe that there is a different mode of production of the same compound in each particular case: on the contrary one would naturally expect the same compound, in whatever place one meets it, to be produced always by the same chemical mechanism."

"Similarly we must admit the possibility of a breaking down of the morphologic signs of species. Morphology is clearly not yet far enough advanced to permit of such an analysis in each particular case. But the same coarse or fine notching at the leaf margins are repeated in numerous species and the customary terminology informs us in advance that all forms of leaf patterns are composed of a relatively small number of more simple characters."

"This shows that the character of each individual species is made up of numerous hereditary peculiarities of which the most part are present also in an almost infinite number of other species. * * * According to this view, we would regard each species as an extremely complicated figure, and the organic world in its entirety as the result of innumerable different permutations and combinations of a relatively small number of factors."

"Experiments upon the production of varieties teaches us further that nearly every peculiarity can vary independently of the others. Many varieties in fact diverge from their stock form by only a single character; for instance the white blooming variety of a species with red flowers. In the same way the villosity, the armanent of spines or thorns, the green color of leaves, each of these characters can vary by itself and can even disappear entirely, and all the other hereditary properties remain perfectly unaltered."

It follows that: "The hereditary anlagen, of which the hereditary peculiarities are the visible signs, are independents units which may have had their origin at different epochs, and which may also be lost independently. They are miscible with one another in almost all proportions, since each peculiarity can pass through all intermediate degrees from its complete absence to its greatest development."

"Independence and miscibility, these are the essential properties of the hereditary anlagen of all organisms." [121]

Quite similar to this argument of DeVries is that of Weismann in favor of his preformation or of preformistic germs in general: "It is impossible for one part of the body to vary independently of the others, and for these variations to be hereditary, if it is not represented in the germ plasm by a special particle, a variation of which induces a corresponding variation of the part in question. If this were represented, together with other parts of the body, by a single particle of the germ plasm, then a change of this latter would have as its consequence the variation of all the parts which are determined by it. In

[121]De Vries: Intracellulare Pangenesis. Jena, Fischer, 1889. P. 8—9, 17, 32, 33. English Translation by C. Stuart Gager. Open Court Publishing Co. 1910.

those parts of the body which are independently and hereditarily variable, we have thus an exact measure for determining the number of the little vital particles which must compose the germ plasm: they cannot be fewer."

"We are then logically forced to assume that a special element exists in the germ plasm for each of these peculiarities, not because the inheritance of even the smallest details is possible, but because each of these parts of the body can have its variations inherited individually, each by itself. If all men possessed a certain depression in front of the ear, one could not conclude that because it was hereditary, it must be represented in the germ plasm by a special element * * * the fact which forces us to accept this hypothesis is that all men do not possess this depression, that we can imagine two people who resemble each other in all other respects but of whom one possesses this depression and the other does not." [122]

This is then the great and only argument of all the theories of preformistic germs.

One cannot fail to see that it really possesses a very great value against such theories as that of Spencer, who supposes the germ plasm to be constituted by a homogeneous substance. In the almost complete darkness in which we still find ourselves in respect to the nature and causes of ontogenetic phenomena, there are very few things which we can venture to call impossible. Nevertheless the supposition which is implied in the epigenetic theories of the Spencer type, namely, that a homogeneous germ substance a little different chemically from an other, is able to give rise to an individual quite identical with that which the other substance produces, except for one little

[122]Weismann: Das Keimplasma. P. 72—74.

peculiarity in a definite part of the organism, if it does not seem quite impossible, certainly seems difficult to conceive. It is true that these theories of the Spencer type can always bring up the objection that to a visible variation of a certain group of cells there might possibly correspond similar variations in all the other cells of the organism, but always so small that they are not appreciable. But such an explanation of the especially inheritable variations would be formal rather than actual.

This applies equally well, it may here be said parenthetically, to evolutionary theories without preformed germs, such for example as the theories which are called those of the chemical development of the egg. They start out usually with a heterogeneous germ substance, constituted by multiple and diverse chemical substances, from chemical interactions of which new chemical compounds are formed later, which give place in their turn,—in each cell as in a separate crucible independent of the others,—to new chemical reactions and consequently to new compounds different in the different cells, and so on up to the end of development. But one cannot conceive how each one of these components of the germ substance, which commences to exercise its chemical action upon the other constituents from the very first moment of development, even though it be the only point in which one germ differs from another, can bring about an alteration of the organism limited to a single point rather than an alteration extended over the entire organism.

The argument brought up by the partisans of preformistic germs, both epigenesists and preformationists properly so called, is then really weighty enough to force us to hold as inadmissible every biogenetic hypothesis which starts out from or is based upon a homogeneous

germinal substance, even though it were as complex as one could imagine; and a germ substance which is heterogeneous indeed but each of whose components would nevertheless commence to be active from the very first moment of development must be no less certainly excluded.

On the other hand we ask: Is it in general possible to conceive, much less accept, these preformistic germs, of which each is set apart for some infinitesimal part of the body,—any part provided that it can vary independently of the others? Would the supposition of germs of this nature constitute any explanation whatever of this particulate inheritance, or would this not rather be a pure and simple repetition in other words of the phenomenon which one pretends to explain?

That is what we propose to consider very briefly in the following last section of this chapter.

4. *Inadmissibility of Preformistic Germs*

We note in advance that the independently variable and inheritable peculiarities of the organism are not limited merely to the form and structure of entire groups of cells, but can include even the chemical characters of each cell. One would arrive thus at the absurdity that not only each cell, as Darwin's pangenesis already admits, but almost each molecule of the organism must have its representative in the germ plasm.

Besides this material impossibility the idea of preformistic germs encounters insurmountable difficulties from the point of view of their conceivability.

Is it a conceivable thing that there is for instance a preformistic germ of a certain nervous tic, or of a par-

ticular instinct, that there is a pangen or a group of pangens for the instinct of the hunting dog, that there is a determinant or group of determinants of the instinct of the new-born chick, which knows already how to peck at the wheat and swallow it? How can we conceive of these instincts which are the consequences of very complicated combinations and interconnections of almost innumerable centers and nerve tracts, as due to one separate germ, which having come up at the opportune moment of ontogeny, and at the exact point of the organism, produces them by itself, automatically, and we may say independently of all the rest of the organism already formed?

And yet these instincts actually constitute variable and inheritable peculiarities of the organism, susceptible of being present or absent independently of all the other peculiarities of the organism. But if, in order to explain this "particulate inheritance" one has recourse to germs especially preformed just for this, would this constitute anything else than a purely verbal explanation without any real inherent significance?

"A man, for example," Le Dantec very rightly says, "is composed of about sixty trillions of cells, and he is nevertheless reproduced by sexual elements of very small size: this is the phenomenon to be explained. It has been thought that the difficulty would be less, or at least would not appear so distinctly, if one were to divide the problem into sixty trillion parts, if one could replace the reproduction of the man by sixty trillions partial reproductions; and there have been consequently imagined infinitely small particles which are to the cells as the whole germinal substance is to the man." [123]

[123]Le Dantec: Traité de Biologie. P. 224—225.

The consequence of this has been that the problem has become enormously complicated because it has given birth to this other very great problem: How comes it that these sixty trillions of autonomous and therefore independent individual parts can constitute a complete and harmonious whole?

It results from this that preformistic germs, which by themselves are quite inadmissible, become yet more so when they are separated from preformistic doctrines properly so called. And Weismann endeavored to show that they are inseparable.

"DeVries," he says, "once mentions the zebra stripes. How can such a character be transmissible if in the germ the different pangens are free one beside another, without being bound up into firm groups inheritable as such? Zebra-pangens cannot give it, for the striping of the zebra is no cell character. Perhaps there are pangens which for brevity we can call "whites" or "blacks," whose presence would produce white or black color in the cell. But the striping of the zebra does not consist in the development of the black or of the white in the interior of the cell, but rather in regular alternations of thousands of black or white cells arranged so as to form stripes."

"DeVries mentions also the long stemmed variety of the alpine Primula acaulis occasionally produced by atavistic return to a remote stem form. Here again the character of the long stem cannot be due to 'long stem pangens,' because the long stem is not an intracellular property; neither is the specific form of the leaves, etc.; the dentate border of a leaf cannot be due to the presence of 'dentate pangens,' but is due to a special arrangement of the marginal cells. The same is true of nearly all the characters which we designate as visible properties of the

species, genus, or family etc., and so of the size, structure, and shape of a leaf, of the characteristic and often constant spots upon the leaflets of flowers (orchids, and so on). All these properties manifest themselves only by the orderly cooperation of many cells. Or think of the properties of the human individual, of the form of the skull, of the nose, and so on. All these very characteristic properties cannot be due only to the presence in the germ of pangens which must form the hundreds and thousands of different cells which compose the property in question; they must be due rather to a fixed grouping of the pangens or of some other corresponding primary element of the protoplasm, transmissible in its fixity from generation to generation." [124]

But when under the pressure of logical necessity we pass from simple preformistic germs, either free or intermingled in any way, to germs built up together into a fixed structure, we fall at once into all the difficulties and contradictions of pure Weismannian preformation, which we have already discussed, beginning with the one which we have seen to present itself first, namely that it is quite inexplicable how this "fixed grouping of the pangens" can divide in successive germ plasms and nevertheless remain unaltered in its structure.

Preformed germs, materially impossible and theoretically inconceivable, are nothing else than empty, wordy names, and appear besides to be quite incapable of explaining even the most important phenomena of particulate inheritance on account of which they were especially devised, and which constitute the only excuse for their existence, when once they are separated from the stronger

[124]Weismann: Das Keimplasma. P. 22—23.

preformistic theories, the absolute inadmissibility of which we have seen above.

* * *

What conclusion can be drawn from the last two sections of the present chapter?

The penultimate section has shown us that the actual independence in variation and inheritance of the various and particular characters of all the rest of the organism can be explained neither by a homogeneous germ substance, nor by a heterogeneous germ substance of which all the various constituents would become active from the first moment of development. The last section has demonstrated to us the inadmissibility of preformistic germs although at first they appear to constitute the most immediate explanation of the mutual independence of the various particular characters.

It remains then for us to see if a heterogeneous germ substance without preformistic germs, but whose constituent parts instead of entering all into action from the first moment of development, become active successively from the commencement to the end of development, can give the adequate explanation of particulate inheritance which we are seeking.

Let us consider first the phenomena of particulate inheritance which are shown by the presence in the child of certain paternal characters simultaneously with other maternal characters, intermingled but yet clearly distinguishable from one another. For the sake of clearness we shall overlook for the moment all sexual peculiarities and limit ourselves to considering only the clearly asexual paternal and maternal characters. "The form of the skull," remarks Weismann for instance, "can be paternal and the face maternal; the form of the entire head and

the face can be maternal and the eyes, in spite of that, be entirely paternal in character; the dimple which the father had on his chin may be found again in the child, although in the form of its face and nose it may resemble the mother rather than the father." [125]

Let us note at the same time that the germ substance of the fertilized egg must contain the anlagen of both the paternal and maternal germ substance, and that the former as well as the latter, since they correspond one to another in pairs, tend to become active in pairs simultaneously or almost simultaneously, except in the cases where they are of such nature as to be reciprocally exclusive.

Now if we suppose that the process may be of epigenetic nature, and if we suppose also that the different anlagen of the germ substance becoming successively active, are all located in one definite zone of the organism from which they send forth their formative action, then it is clear that the different points of the soma must experience the determinative influence of the paternal and maternal germinal anlagen at the same time.

Consequently when the corresponding anlagen composing each couple are quite identical, as will be the case especially during the first stages of development and perhaps also at subsequent stages more or less advanced, then the two respective, determinative actions will become fused into one, and there would result the exact reproduction of the entirely similar characters which the two parents possess in common.

When on the contrary the corresponding anlagen composing each pair are different, provided that they are not,

[125]Weismann: Das Keimplasma. P. 377.

we repeat, different to such a degree that the activation of one prevents that of the other, the two formative actions will be likewise different for all the points of the soma upon which their action would be perferably or exclusively directed, and they would be able thus either to combine and thus unite into a single resultant formative action, or, by developing their respective characters separately, to bring about an intimate interlacing of them, in such a way as to cause the appearance of a commingled intermediate character, or finally the paternal character developed by one of the formative actions can at a given point prevail over the maternal to such an extent as to appear in all its purity, while perhaps the reverse appears in a neighboring point of the soma, and the maternal character comes alone to development.

A characteristic example of this interlacement of paternal and maternal characters remaining in part distinct but in part fused, is shown us by the hybrid arising from the spontaneous crossing of Vitis aestivalis and Vitis labrusca, the epidermis of whose leaves is formed like a mosaic, the cells of which belong either to the purely paternal type or to the purely maternal type, or to an intermediate form.[126]

If now after considering the phenomena of particulate inheritance due to sexual reproduction, we consider the phenomena of this particulate inheritance in its broadest extent and most general significance in order to be able to answer the question; how can the simple fact be explained that two individuals can be altogether alike except for a single definite peculiarity at a single given point of the

[126]Strasburger: Über periodische Reduktion der Chromosomenzahl im Entwicklungsgang der Organismen. Biol. Centralbl., Bd., XIV. No. 23 and 24, Dec. 1. and 15, 1894. P. 850.

organism? It will not be difficult to convince us that the possibility of this phenomenon will be fully provided for by the same hypothesis of the structure of the germ substance which has served to explain for us the same phenomenon in so far as it is due to sexual reproduction.

Let us imagine, for example, two germinal substances constituted by two series of specific anlagen, which are qualitatively alike, but in one of which a certain entire group of these anlagen is furnished with a little less potential energy than in the other. We do not need to suppose, even though we could, that this certain group of specific anlagen is of such a nature that its activation in the above mentioned common zone from which formative stimuli are given out should determine preferably or exclusively just that part of the organism which shows itself capable of independent variation, such as for example the dimple in front of the ear of which Weismann speaks. Instead we could very well suppose that this group, either by itself or in combination with others, brings about definite ontogenetic modifications not only in this one part but also in many other parts, perhaps even in all the cells of the organism without exception. But the epigenetic nature which we attribute to the process of development implies the idea that the activation at a given stage of ontogeny of a definite specific anlage must exert very different influences not only qualitatively but quantitatively upon the individual parts of the soma that are already formed. It is thus conceivable that a very small amount of potential energy in a given group of specific germinal anlagen might exert inappreciable effects or indeed no effect at all on a definite or even great part of the organism, but yet exert quite an appreciable or even considerable effect upon another very

small part of it, and so much the more since the effects produced by this particular group of germinal anlagen must combine with those produced by all the others both antecedent and subsequent.

It would amount to the same thing if this given group of specific anlagen differed from the corresponding group of the other germinal substance not only quantitatively but also qualitatively to a certain extent.

We believe the final result to be that we can affirm that the hypothesis of a heterogeneous germinal substance whose anlagen do not all enter into action from the first moment of development, but rather become active successively one by one, throughout the entire course of development, explains the phenomena for which preformistic germs were especially devised quite as satisfactorily as they do, and at the same time is not open to any of the formidable objections, which demonstate with certainty the untenability of the hypothesis of preformistic germs.

CHAPTER FIVE

THE QUESTION OF THE INHERITANCE OF ACQUIRED CHARACTERS

The great service of Weismann, which is not yet appreciated highly enough, is that he brought forward this matter of the inheritance of acquired characters, and questioned its existence, which previously had been not only tacitly admitted by most biologists, but regarded as not needing proof. And we must recognize the fact that the great and justifiable desire to find for this inheritance some proof which should be irrefutable and not open to any objections has remained so far unfulfilled.

It is not proposed here to make a long list of all the facts which have been brought forward as proofs of the Lamarckian principle, but it will be worth while to examine a few in order to show clearly that Weismann and his school are not really far wrong in denying to most of these facts any right to be considered conclusive proof.

We shall leave aside the question as to whether calves have really been born without horns, as alleged, in consequence of the breaking off before their conception of the horns of one or other parent; or whether tailless calves were produced by a bull whose tail had been squeezed off at the root by the violent closing of the stable door. It is clear that all these cases and many others like them, which have been reported in dogs, cats, rats, and

so on, can not constitute any satisfactory proof in the absence of reliable observation and confirmation of the facts.

Darwin draws especial attention to the inheritance of characters acquired by domestic animals. "The domesticated duck," he remarks, "flies less and walks more than the wild duck and the bones of its anterior and posterior limbs have become respectively diminished and increased in comparison with those of the wild duck. A horse is trained to certain paces and the colt inherits similar consensual movements. The domesticated rabbit becomes tame from close confinement; the dog intelligent from associating with man; the retriever is taught to fetch and carry; and these mental endowments and bodily powers are all inherited." [127]

These examples, one must admit, deserve all consideration, especially the first. But one encounters here the objection which can always be raised against such examples: As functional adaptation has a great modifying influence upon the organism, how can we be certain that the greater size of the bones of the legs in the domestic duck really springs from inheritance of acquired characters rather than from the daily exercise of the individual itself? Would not a wild duck if it were obliged to walk during all its life from its coming out of the egg acquire a similar hypertrophy of these bones? Unfortunately we have not exact measurements on this point which alone could decide the question whether hypertrophy acquired during the life of an individual could attain the same degree as that which has been observed in the domestic duck.

Several travellers have remarked that when men have

[127]Darwin: The Variation of Animals and Plants under Vol. II. P. 367.

disembarked for the first time upon uninhabited islands the animals have not often any fear of them, but after a very few generations the fear of man has become an inborn instinct.

Weismann and his followers could object here also that this fear of man is not even now an inborn character, but rather is simply acquired after birth and due to the education, in the largest sense, which the little animals continually receive from their parents and from all the other adults merely by observation and imitation of their conduct on definite occasions.

"The co-ordination, arrangement, and connections of the ganglion cells which innervate the muscles of speech," says Roux, "are already inborn in us to such an extent that we learn to speak our mother language easiest, while for example Europeans even when brought among the Namas while still children never learn their language as perfectly as the Namas themselves, or do so only with the greatest difficulty." [128]

This does not prevent any one fundamentally opposed to the inheritance of acquired characters from objecting that the European language spoken by the parents and ancestors of the child may not be the cause of these dispositions and inborn connections of the ganglion cells but rather the effect; in other words, it is not the use of this or that speech which develops such and such inheritable connections; but rather the presence of certain connections due to natural selection has produced certain peculiarities in the character of the language of a given human race.

"When young hunting dogs," writes Exner, "which

[128]Roux: Der Kampf der Teile im Organismus. P. 38.

have never been out hunting, nor had occasion to become otherwise acquainted with guns and their effects, hear one in the fields for the first time they start up eagerly, just like old hunting dogs, to retrieve the prey even when they do not see any fall. This demonstrates that since the invention of gunpowder the mnemonic image of a gunshot and its effects has passed hereditarily into the brain of the dog, and so has been gathered up in the so called instinct." [129]

And here, we do not really know what objection the Neo-Darwinians could bring forward; for it seems to us that they would encounter difficulties in trying to attribute the formation of this instinct in a brain which was absolutely *tabula rasa* in so far as this instinct is concerned, to the artificial selection of the breeders. We must nevertheless recognize that even this example does not fulfill, and cannot from the nature of it fulfill all the requisite conditions of exact observation, of measurement, of control, and particularly of comparison which alone could give a single case the value of a decisive proof.

A very remarkable example is reported by LeDantec. The shells of Hyatt's oldest cephalopods have the form of a cows horn nearly circular in transverse section. And following the series of these fossils in the more recent strata, one notes that these shells, at first almost straight, are little by little rolled up upon themselves like an Archimedes' spiral. The presence of certain characters shows clearly that the rolled up forms are descended from those with the straight shell. In a few types the rolling up is so marked that the successive turns of the spiral press one

[129] Exner: Physiologie der Groβhirnrinde, in Hermann: Handbuch der Physiologie. Zw. Bd., Zw. Teil. Leipzig, Vogel, 1879. P. 282—283.

into another, giving rise to a dorsal groove the mechanical production of which is evident since it undoubtedly results from the pressure of the preceding spiral upon the succeeding. Now in a still more recent geological period paleontological discoveries show that the descendants of these cephalopods with a tightly rolled up shell have begun to unroll, and have then the form of an Archimedes, spiral with broader turns which no longer touch one another. But the dorsal groove persists even in these half rolled up shells, a proof that the younger cephalopods have repeated hereditarily this character which was acquired by their ancestors.[130]

This is certainly a most interesting example, but it has not quite the force of complete proof. For besides the objection, which we shall examine later, that the groove is formed in the non-living substance of the shell, it does not exclude the interpretation, though it be only verbal and without any real foundation, that it was not the rolling up of the spiral upon itself that produced the inherited groove, but rather that both the tight rolling up and the groove were selected and fixed independently of one another by natural selection.

The influence of dry, hot climates upon the development of the horns of cattle and sheep is well known. If certain individuals of a certain breed of cattle are transported from a wet, cold climate to a hot dry climate, the horns increase in length and circumference and the skin thickens. The following fact seems to prove that this acquired elongation of the horns is inheritable. A cow was transported from Algau in Bavaria where the climate is moist and cold, into the dryer and hotter steppes of

[130]Le Dantec: Traité de Biologie. P. 296—297.

Hungary. This cow whose horns were 19 cm. long gave birth to a calf with horns 22 cm. long. The calf of this calf born also in Hungary, (presumably from a father of the same race as that of the mother?) had horns 23 cm. long and thicker than those of its mother and grandmother.[131]

So of the three centimeters of elongation, due to the action of the environment, which we can regard as functional adaptation in the widest sense, one centimeter would have become hereditary in a single generation. It is however evident that experiments of this nature cannot have any real significance unless they are made on a large scale, so that an average can be established from many instances. And this experiment of Wilckens has been mentioned here just because the way in which it was conducted comes close to possessing the requisite and indispensable conditions of a fundamental proof.

Another instance which the partisans of the inheritability of acquired characters adduce is brought forward by Spencer: it is that of the Punjabi of India, who have certain muscle imprints on the bones of the leg, and certain facets in the articulations of the hip, knee and foot, which are produced by their habit of squatting upon the ground; and these peculiarities are hereditary, as is demonstrated by the fact that they commence to show themselves even in the foetus.

Weismann seeks to demonstrate that they are only the continuation in man of certain peculiarities in the articulations of anthropoid apes which natural selection had already fixed in very ancient times because they

[131] Wilckens: Die Theorie erworbener Eigenschaften vom Standpunkte der landwirtschaftlichen Tierzucht in Bezug auf Weismanns Theorie der Vererbung. Biol. Zentralbl., July 15, 1893. P. 426.

were useful then. But still, in our opinion, he has not been able to explain correctly why these peculiarities are retained only in the Punjabi, who are also the only ones of all the tribes of the same family who are accustomed to squat in this way.[132]

One could bring up also as examples the callosities at the knees and sternum which are hereditary in the domestic camels but are lacking in the wild camels. Thus for example the camels of the tame stock of San Rossore near Pisa (Italy) are covered with hair both over the breast bone and on the knee at birth, but after a few days they lose the hair in the breast bone region, which is then permanently replaced by a horny plate. Every camel up to three months old had these more or less broad, hairless plates, though they still retained the hair on the knee, but the thickened and hardened skin could be felt under it. Of course these camels which were only a few months old were not required to do any work. On wild camels, on the contrary, no such swellings are to be found either in the very young or the adult.[133]

Still more remarkable is the following fact reported in 1888 by Prof. Fogliata. "A she ass from the Tuscan Appenines, which long had borne the pack saddle, showed on the back and on both sides over the ribs, a very evident pad of soft fat, which in extent and shape was like those which the pressure of an ordinary mountain pack saddle produces. This she ass was put to an ordi-

[132]Weismann: Neue Gedanken zur Vererbungsfrage. Eine Antwort an Herbert Spencer. Jena, Fischer, 1895. P. 54ff.

[133]Cattaneo: Le gobbe e le callosità dei cammelli in rapporto colla questione della ereditarietà dei caratteri acquisiti. Estratto dai Rendiconti del R. Istituto Lombardo di sc. e lettere. Serie II, Bd. XXIX, 1896. P. 10—11; and: I fattori della Evoluzione Biologica. Genua, Martini, 1897. P. 40—41.

nary male ass and bore a female colt which shows the same peculiarity as the mother. Its fat pad which covers the back and reaches almost half way down the ribs is not less than 5 cm. thick, clearly defined, and has an abrupt and perpendicular margin. It is to some extent a distinct and separate fat mass,—a true lipoma,—certainly similar to those which according to Lombroso's description are produced by burden bearing. It has the same character as the hump of the camel, is more or less developed according to the condition of nutrition of the animal, and appears exactly as though it had arisen by the pressure exerted by a saddle on the back. Also the hair is longer and thicker over the whole of the fat layer, which agrees likewise with the observations of Lombroso on pack animals possessing such lipomas, and is like the hump of camels also, which is covered with thicker, longer wool. It is worthy of remark that this young she ass has never borne a saddle and inherits its peculiarity entirely from the mother, which proves beyond doubt, that this peculiarity, acquired by pressure on the back, has been inherited.[134]

Even though this single fact cannot decide the question finally we do not really see what objection Weismann and his school could urge against it.

Finally we have the celebrated experiments of Brown Sequard on guinea pigs, proving the transmissibility to the young of effects produced in the parents by certain accidental lesions.

Thus he has demonstrated that epilepsy, produced in one of the parents by section of the sciatic nerve or of a part of the spinal cord, is transmissible to the young.

[134]Cattaneo: Le gobbe e le callosità dei cammelli etc. P. 9—10.

After section of the sympathetic trunk in the neck there was produced a particular change in the form of the ear or a partial closing of the eyelids, and the same modification of the ear, and the same closure of the eyelid were reported in their respective descendants.

A lesion of the medulla oblongata produced exophthalmos in certain guinea pigs and the same exophthalmos showed itself in the young.

Ecchymoses accompanied by dry gangrene and other alterations of the nutrition of the ear have been reported in the descendants of individuals in which this series of phenomena had been produced by a lesion of the restiform body.

Certain other guinea pigs in which section of the sciatic nerve had rendered the hind foot insensible to pain gradually destroyed their toes by gnawing them; it is reported that in their descendants parts of the toes or even whole toes were missing from one of the hind feet.

Other individuals in which the sciatic nerve had been cut had descendants which exhibited at first a diseased condition of the same sciatic nerve, and later the phenomena characteristic of the onset and decline of epilepsy, particularly the development of an epileptogenous capacity in a zone of skin of the head and neck, and a loss of hair toward the decline of the affection.

Guinea pigs which had had an eye altered in consequence of the transverse section of the restiform body had descendants which all showed more or less imperfection in one or both of the two eyes.

In more than a score of guinea pigs representing the total posterity of individuals in which muscular atrophy had developed after section of the sciatic nerve

there appeared just such a muscular atrophy of the thigh and of the leg.[135]

The desperate endeavor which Weismann has made to refute the results of these experiments, at least in relation to the transmissibility of epilepsy, is well known, objecting that this affection was due only to an infection innoculated in the parents after operation and so transmitted to the germ. Brown Sequard has signally overcome this objection by showing that epilepsy is not produced by all nerve sections but only by some, and that further it can be provoked also by the simple crushing of the sciatic nerve without any breaking of the skin, and this would exclude the possibility of any infection whatever.

Nevertheless it is necessary to recognize the fact that these experiments, while they undoubtedly demonstrate the inheritance of the effects of certain lesions, are not enough to produce a firm and general conviction of the inheritance of acquired characters among the numerous naturalists and biologists who are in no wise blind followers of Weismann's theories; perhaps because what is inherited in these cases is always somewhat morbid and abnormal. In short the determination of the question requires certain proof of the inheritance of definite normal peculiarities acquired by functional adaptation.

We see then, that whoever proposes systematically to hunt out a weak point in every fact adduced in support of the Lemarckian principle, by which its value as proof can be shaken, can usually if not always find it. But

[135]Brown Séquard: Faits nouveaux établissant l'extrême fréquence de la transmission, par hérédité, d'états organiques morbides, produits accidentellement chez des ascendants. Comptes Rendus de l'Acad. der Sciences. T. XCIV, No. 11, March 13, 1882. P. 697—700.

this would justify the assertion that the inheritance of acquired characters has not yet been directly proven, only in the case that there were but a few facts or only a single fact that could be brought forward in proof of it. But when on the contrary there are a very large number of facts favorable to a given principle, even though each one of them by itself would not be an absolutely incontestable proof, they would in spite of that have, when taken as a whole, a very great value as proof, and this value would be so much the greater if the opponents of the principle, in seeking to deny the incontestability of the individual facts, are forced to resort to as many specially devised subtleties.

On the other hand the non-inheritance of certain gross instantaneous modifications, such as amputations and other similar things, of which Weismann and his followers make so great a case, proves nothing against the inheritance of functional adaptations which are of quite different nature.

For let us consider the dynamic equilibrium existing in the adult state in a given small portion of the soma, and let us suppose also that this equilibrium was established by a process of epigenetic nature dependent upon all the rest of the organism. If this local equilibrium is suddenly very much disturbed as is the case in amputations, instead of gradually and slowly as in functional adaptations, one can understand that it can and must be promptly restored in the neighborhood of the wound or in any case in the limited area of the stump, before the disturbance has time to extend much farther. Therefore if there is a definite place in the organism to which non-transitory derangements and the variations of equilibrium caused thereby must

penetrate if the corresponding morphological modification is to be inheritable, it follows that amputations, unlike functional adaptations, could not as a rule leave any trace of themselves in the descendants.

But in still another very essential point amputations are different from functional adaptation. The amputation of a limb, or of a piece of a tail, does not constitute in any way the mode of reaction of the organism to a definite external influence, but rather it is this external influence itself. How then will its reproduction in the new organism be possible? This would be the same thing as expecting that an individual who had been accustomed throughout his life to bear a burden upon his shoulders as exercise, should transmit to his son not only stronger bones and muscles but also the burden itself which was the cause of this strengthening.

So that the most that could be transmitted to the descendants of an animal which had undergone some amputation, would be the mode of reaction of the organism to this gross external influence, that is all the phenomena constituting the cicatrization, properly so called, of the wound, as well as the establishment of a new local equilibrium. We must however bear in mind in this connection that the reproduction in the child of considerably thicker and stronger bones and muscles will not be hindered by the fact that it is not exposed to the same external influence which acted upon the parent, i. e. by the fact that it does not bear the same burden as its father, but that if one does not also repeat the amputation, the repetition of all the phenomena constituting the cicatrization of the wound and the reestablishment of a new equilibrium could not but be very much hindered and usually quite prevented by the pres-

ence of the limb or other part of the body which was destroyed in the parent.

In order to make this more apparent let us consider some one of the numerous rats from which Weismann cut off the tails, and which that author has rightly brought forward as proving that the surgical operation of amputation is not inherited. Let us suppose that in the young rat when once his development was completed and he had arrived at about the age at which the old rat had undergone the amputation, really showed at the spot at which the amputation took place a tendency to reproduce the same phenomena of cicatrization and reestablishment of the new local equilibrium which had supervened in the parent. It is evident that the absence of the tail is a necessary condition in order to make the reproduction of these phenomena materially possible. This tendency must then be hindered and perhaps absolutely suppressed so long as the tail remains a part of the organism.

It is interesting in this connection to note that Kohlwey has obtained in one and the same individual a completely negative result in respect to the inheritance of mutilations, but a positive result in respect to the transmission of habit: He cut off the posterior digit from the feet of some pigeons which thereupon turned back another digit in order to retain their perch; and in one instance this habit was reproduced.[136]

The decisive experiment upon the inheritance of acquired characters must leave amputations and similar sudden variations out of consideration, since either their effect is to bring about the reestablishment of an exclu-

[136]H. Kohlwey: Arten und Rassenbildung. Eine Einführung in das Gebiet der Tierzucht. Leipzig, Engelmann, 1897, P. 6—7.

sively local equilibrium or the repetition in the descendants of the phenomena by which the parent organism reacted is hindered. This experiment must rather be directed toward modifications of the functional adaptation, wihch have a very extensive action and whose repetition in the descendants is not hindered by anything.

In order that these experiments on the changes dependent upon functional adaptation may constitute an incontestable proof for or against the inheritance of acquired characters,—which latter are to be understood in Weismann's sense as only somatic and not general peculiarities of the entire organism,—they must be planned in such a way as to make it certain that the change effected by the transforming influence has affected only the soma directly, and for still greater certainty it ought to act upon only a definite part of the soma and not upon the entire soma to the same extent. They must also be undertaken on pluricellular organisms in which the somatic germ cells are clearly differentiated, and there ought to be employed as transforming influences only such as certainly exert no direct influence upon the reproductive cells.[137]

All plants in which the difference between somatic and germ cells is not a thorough going and definite one will therefore be less suitable for these researches than animals, and particularly higher animals, and all such investigations both in animals and in plants which employ physical or chemical transforming agents exerting a general action on the entire organism, on the somatic cells as well as on the germ cells, as for example tem-

[137]Compare J. De Meyer: L'hérédité des caractères acquis est-elle expérimentalement vérifiable? Archives de Biologie. Tome XXI, No. III and IV. Paris, Masson 1905, P. 625, 634—639.

perature, light or darkness, particular substances that are nutritive, stimulating or poisonous, infections, immunizations, etc., could never afford such incontestable evidence against Weismann's theory, as those investigations which employ agents having a very definitely localized action.

Thus for example Heschenhagen's researches upon the adaptability of the lower fungi to sodium chloride have, for the reasons stated, little or no value for the refutation of Weismann's theory, even though they have proved that the spores of the mycelium which had adapted itself to a strongly concentrated saline solution were capable of germinating in concentrations in which the spores of a mycelium arising in normal conditions were incapable of germinating. The same is true for the similar researches carried on by Hunger-Errera, DeMeyer, Pulst and Ray upon the inheritance of changes, mostly physiological rather than morphological in nature, which were brought about in the lower fungi by means of concentrated salt solutions, for example by sodium chloride or copper sulphate or concentrated sugar solutions, although these results as well as Heschenhagen's are certainly very interesting from the point of view of the adaptability of organisms to their environment.

Also Hoffman's researches upon the inheritance of variations produced by insufficient nourishment in Papaver, Migella, and Argemone,—(a relatively large number of atypical flowers),— and Schubeler's researches upon the inheritance of the more rapid development of barley grains which had been transplanted from the south part of Norway to the north part, prove incontrovertibly the inheritance of the changes induced in organisms through general conditions in their environment, but the general influences very probably exerted in those cases also

by the selected transforming agent upon the whole organism, and our entire ignorance of the real nature of its peculiar action, deprive these experiments of any value as arguments against the theory of Weismann which denies the inheritance of any peculiarly somatic characters that have been acquired by means of local functional adaptation to external influences that are very definitely and clearly limited.

Just as little valuable as proof against Weismann's theories were the researches of Standfuss, Fischer, and Bachmetjeff on the inheritance of changes in the color design of butterflies' wings, when the pupae concerned were placed in an unusually high or low temperature, so that Weismann, as we shall see further in the next chapter, could acknowledge the otherwise unimpeachable results of these researches without thereby being compelled to retrench his own theory.

It would be best therefore to employ mechanical means, and to produce changes whose mode and place of working can be easily observed and definitely limited. But amputations are to be excluded for the reasons given, as are also sudden transformations, and so there remains as the experiments best adapted for the final decision of this disputed question, prolongation or frequent repetition of the activity of certain organs or definite parts of organs.

We might suggest for example the artificial and therefore extraordinarily frequent extension or contraction of the muscles of the fore or hind legs of a certain animal, such as could be effected in little amphibia or little mammals with the help of an especially devised clock work. Prolonged traction on the tail of the rat leading to its elongation and growth should be substituted

for Weismann's amputation which can prove nothing. Similarly light hammering, continually repeated, which a proper mechanism might automatically perform upon certain parts of the skull of hornless animals, would be better than cutting off or breaking the horns in horned animals.

All these artificial stimuli would certainly produce in each individual the hypertrophy of the organ upon which they act. It could then be seen whether the repetition of these stimuli throughout a series of generations would be followed by the production of individuals in which these organs would possess at birth even in a small proportion the greater development that had been acquired in several successive generations of its ancestors. The performance of such experiments upon guinea pigs or rats would not seem to present very great practical difficulties; nevertheless, so far as we know, it has never yet occurred to any one to make them or to propose them.

But in all these experiments one must never forget that it is just the littleness of the inheritable fraction of an acquired quantitative variation, that constitutes the great difficulty of verification of the Lamarckian principle.

Galton proposes as is known to select for experiment rather the inheritance or non-inheritance of certain acquired instincts. He advises for example to adopt the method of the following experiment of Möbius upon the pike; Möbius divided a large glass receptacle into two compartments by means of a perfectly transparent glass septum and placed the pike in one compartment and in the other little gudgeons upon which the pike usually feeds. It followed that whenever the pike precipitated himself toward any of the little fishes he was stopped by the glass against which he hit. After several weeks of

useless attempts the pike finally gave up any attempt to catch this unseizable prey and he persisted in this attitude even after the glass had been removed. Now Galton advises repeating this same experiment on several generations of pikes, taking care that each generation should always be brought up apart from the preceding to prevent any possibility of the educative influence of imitation, and seeing if one would finally obtain any descendant in which the instinct to throw himself upon the gudgeons would be replaced by the contrary instinct of indifference toward them.[138]

We should remark in this connection that because one is here concerned with establishing the transmission of an acquired instinct that is opposed to the inborn instinct, experiments of this nature are less advisable than those which seek rather to verify the inheritance of a simple quantitative increase acquired by already existing organs or tendencies. In Galton's experiment the tendency of the descendants to produce the new instinct even if it were present through a long series of generations, might not possess sufficient potential energy to enable it to manifest itself through activation because it would have to overcome a pre-existing tendency which in the beginning at any rate is certainly furnished with a greater quantity of potential energy. Therefore it is probable that it would be necessary to submit a very long series of generations to this experiment of the glass partition before the new tendency would be able to attain a superiority over the former and to replace it. The first pike upon which Möbius made his experiment

[138]Galton: Feasible Experiments on the Possibility of transmitting acquired Habits by Means of Inheritance. Paper read at the British Association. Nature, October 17, 1889. P. 610.

furnishes us itself a proof of this. For from the first impact against the glass partition the inclination contrary to its instinct must have commenced to arise; nevertheless it effected the replacement of the latter only after a large number of unavailing attempts.

From all that we have said thus far it follows that it is much to be desired that new and absolutely incontestable experiments should once for all finally place the inheritance of acquired characters beyond a doubt. But it also follows, as we have said, that if no one of the proofs which we possess already demonstrates this inheritance in an absolutely certain way, nevertheless all together they supply a great weight of evidence for it. As we shall see later this is true also of indirect proofs; one cannot say of any one of them that it decides the question in one way or the other, but all together they constitute a strong presumption in favor of the Lamarckian theory.

It will be convenient to examine next the chief arguments which Weismann has adduced against this theory. They can be reduced in substance to the following:

1. "In many animals," he writes, "for instance in many insects, instincts appear which are exercised only once during life. It is sufficient to cite the laying of eggs by ephemerids and many butterflies, the conjugation of bees, the search for proper hiding places in which caterpillars may change into chrysalids,—one species suspends itself, another lying on the ground builds defences, a third goes deep into the earth, a fourth spins itself a case in a rolled up leaf, and so on, and so on. Further there belong here the several species of cocoons which some butterflies, especially the bombycids, spin in a fashion so astonishingly complicated and so well

adapted to its purpose, a thing which each individual does only once and from the most ancient times has done only a single time in all its life." [139]

2. The second group of facts controverting the inheritance of acquired characters is furnished, according to Weismann, by the parts which have only a passive function, "in so far as they show that they also become rudimentary and finally disappear if they cease to be used and are not necessary for the preservation of the species. They show that the process of disappearance which the Lamarckians attribute to the inheritance of the direct effects of non-usage cannot be due to this cause, since here the organ in question does not exert any physiological function and so there are of course no effects of such function in the individual life. To this category belong for example the colors of animals, which become unstable when they are no longer needed for protection or as a means of recognition; here also belongs the deterioration of the chitinous cuirass of various crustaceans and insects which thrust one part of their body into protective envelopes." [140]

3. The third argument against the inheritance of acquired characters is that constituted by the neutral individuals among bees, ants, and termites which, according to Weismann, show that all the adaptations whether positive or negative, isolated or co-ordinated, that are to be observed in propagating individuals, appear also in individuals which do not propagate at all and which therefore do not transmit anything.[141]

[139]Weismann: Neue Gedanken zur Vererbungsfrage. Eine Antwort an Herbert Spencer. P. 61—62.

[140]Weismann: Ibid. P. 62—63.

[141]Weismann: Ibid. P. 66.

4. Finally the last argument of Weismann is that it is incomprehensible how the inheritance of acquired characters could be effected.[142]

In the endeavor to examine these four arguments with the most scrupulous objectivity, we must first divide them into two categories: The fourth is the only one which attacks the principle of inheritance directly; the first, the second, and the third, on the contrary, controvert this theory only indirectly, in that they seek to show that many formations are of such a nature or arose under such circumstances that they can be explained only by the theory of natural selection. The conclusion which it is desired to have drawn from this is clear, and is indeed admitted: If natural selection is capable of explaining some formations it will be capable also of explaining all the others; if all formations can be explained by natural selection alone, the inheritance of acquired characters becomes useless for the purpose of explaining the transformation of species; consequently if it is useless it is very probable that it does not exist at all.

The impartial reader will admit that this manner of reasoning is deceptive. Even if it be proved that natural selection must necessarily have been capable of producing certain formations with the help of fortuitous individual variations, it does not follow that it must also have been capable of producing all other phylogenetic formations, especially if they are different in nature from the former. And even if the proof were forthcoming that it is capable of explaining by itself all phylogenetic formations whatever, it is evident that even this would not constitute

[142]Weismann: Ibid. P. 61.

any argument against the inheritance of acquired characters. The continuous electric current for example can be produced by a battery as well as by a dynamo; and the fact that one can always explain it as having been produced by a battery does not prevent it from being actually produced by a dynamo in many cases.

This being so, let us now examine as succinctly and objectively as we can each of the four arguments:

1. No value can be attributed to the fact of the exercise of a function only a single time during life. In the first place, it is possible that it may formerly have been exercised repeatedly by the ancestors of individuals now living. In the second place this singleness does not exclude in any way its inheritance as a habit acquired by exercise. For the fact of having performed a given function even though only a single time, would certainly leave in the parent organism a potential disposition to perform it again and with greater facility in similar physiological and external circumstances; therefore the conception that this disposition and this greater facility would be represented in descendent organisms represents only an ordinary case of inheritance.

2. As for the second argument one cannot but recognize that for certain formations the statement of Weismann that they can be due only to natural selection seems very probably true.

But it must be remarked that to support his assertion Weismann attributes a merely passive function to many parts in which it is very questionable.

Why for instance should we not regard the carapace of the turtle as a true and functional adaptation due to the stimulus of the environment to which the skin of the animal had reacted by a secretion constantly richer

in hard substance, exactly as the skin of the sheep reacts by the secretion of wool? There is nothing to prevent such secretions, produced through functional adaptations, serving later as protective shields and thus becoming useful to the species in still another way.

On the other hand the envelopes into which the crustaceans and insects cited by Weismann insert one part of their body might preserve the external surface of that part from the hardening action of external agents, just as houses and clothes may have contributed to the disappearance of the hair in man. For one should not consider the passive function of the hair or of the chitinous substance so much as the active function of the tissues which secrete these substances; and this function is essentially active for it is a specific reaction to external influences.

In this respect the hermit crab constitutes one of the most conclusive proofs of the Lamarckian theory. For this crab which is accustomed to insert the hinder part of his body into empty snail shells has completely adapted itself to the conformation of its new habitation, and this bodily adaptation acquired by it has become hereditary so that it is present in advance before the animal inserts itself into its house. According to Weismann's view, the animal must have first adopted the habit and natural selection must have been able to exert its influence only subsequently. Clearly both processes must go on at the same time, the residence in the new habitation and the adaptation to it; and the fact that these exist together can be explained only through functional adaptation and inheritance of its effects.[143]

[143]G. Cattaneo: I fattori della evoluzione biologica. P. 43—45;

Similarly, how can one escape attributing the colors of butterflies' scales to functional adaptation when one sees the golden red butterfly Polyommatus phlaeas change its color and take on a black tint merely from transporting it to warmer climates?

Further, indubitable instances are known in which the color of the environment stimulates the outer surface of the animal directly or indirectly to take on the same color. Thus some arctic animals and birds become perfectly white in winter, putting themselves thus in conformity with the general color of the environment. Certain butterflies present phenomena of protective polychromatism in the sense that they always take on the color of their environment, and this should not appear strange for there is nothing inadmissible in the supposition that a very sensitive skin can suffer much greater discomfort when the light rays which strike it are of a color different from its own than when they are of a like color with it. This discomfort would correspond to the disagreeable sense of heat or cold which makes itself felt over the surface of the body when its temperature differs from that of its environment.

Consequently if every functional adaptation of the living substance to external agents consists in such a modification of its own vital processes that these find in the external agents no longer obstacles but rather cooperative stimuli, one can understand the tendency of every especially sensitive organ to make the color of its surface conform with that of its environment. This would not prevent the identity of colors from being of

and Cesare Lombroso: Ancora dei caratteri acquisiti; Paguri, Cammelli e Zebú. Rivista di Scienze Biologiche. Vol. II, No. 3. 1900. P. 2—3.

service to the animals in a protective way also, but nevertheless the productive cause would remain always a functional adaptation.

From the preceding instances in which the action of the color of the environment upon the external surface of the animal appears to be direct we pass on to those in which this action is indirect. Thus many fishes, amphibians, reptiles and cephalopods are capable of changing their color in a very short time and thus of putting themselves always in accord with the very variable color of the environment. The color of the environment which determines that of the animal does not act nevertheless, in this case, directly upon the elements of the skin, the chromoblasts, which produce the color; but by a complicated nervous apparatus connecting these elements with the part which is first stimulated by the color. This part is sometimes constituted merely by the nerve ends of the skin, at other times by the retinal nerve ends of the eye. In the latter case if the optic lobes of the brain are artificially destroyed the capacity of changing color disappears.[144]

Further, according to LeDantec, many colorations of the skin that are now fixed and correspond to the henceforth unchanging color of the environment are derived from former colors that changed voluntarily with the different colors of the environment, of which one certain color has remained, persisting to the exclusion of all the others.[145]

One could perhaps also adopt the opposite view. Just

[144]Weismann: The Effect of external Influences upon Development. P. 26—27.

[145]Le Dantec: Lamarckiens et Darwiniens. Paris, Alcan, 1904, Chap. XIV: Le mimétisme lamarckien. P. 129—149.

as the secretion of gastric juice was originally a functional adaptation of the wall of the stomach to certain foods but finally is poured out before the foods themselves are ingested but only tasted, in consequence of psychic associations; so the assimilation to the color of the environment, which originally was a functional adaptation of the elements of the skin producing the color, the chromatophores, may have gradually come to be produced in anticipation and finally exclusively by the perception through the eyes of the color of the environment.

However that may be, all these facts show that far from seeing in the protective colors of animals merely the result of fortuitous variations which have become fixed by natural selection just for their passive protective function, we have legitimate reason for holding on the contrary that usually they are the direct result of true functional adaptation.

In this way would be explained the possibility that as soon as the color of the environment alters, the protective color of the animal might also become unstable or disappear entirely, and one would not be compelled to resort for the explanation of the phenomenon, as Weismann is, to panmyxia or to any other complicated process of natural selection. For this tendency to give up the color can in this case also be attributed to the simple circumstance that when the color of the environment was altered the functional stimulus ceased, which was the sole cause of the color of the animal.

It is true that Weismann points out certain cases of more typical mimicry which seem to prove the correctness of his views very especially because they seem to show that natural selection had undoubtedly been

alone sufficient to produce in some instances extraordinarily complicated formations down to the most minute peculiarities. The example of Kallima, a well known leaf-like butterfly, will at once occur to every one. Nevertheless it is known that certain Lamarckians have had the hardihood to wish to attribute these very perfect resemblances to former, voluntary, chromoblastic, mimetic changes which do not now exist in the animal but which can be demonstrated even now in certain other animals, for instance in some fishes. The absence of change in the object taken as a model which was imitated only voluntarily at first, has resulted in the gradual withdrawal of the imitative color mechanism from the control of the animal's will.[146] Here it is sufficient to remark that the last word has certainly not yet been said upon this voluntary mimicry which rightly excites the greatest interest. In any case such imitative formations as that of Kallima cannot be disposed of by simply referring them to natural selection alone, seeing that their protective utility can commence to be manifested only after they have attained an advanced degree of perfection.

"A muscle," insists Weismann, "can become greater by use, but a claw, a bristle border, a dentition, a protuberance at an articulation, cannot become thicker, longer or stronger by usage, it can only be used up." [147] But does not the very use of these inactive parts or, better, the transmission through the inert substance to the living substance of the mechanical action constituted by this repeated use, provoke the living tissue to secrete in larger quantity the chitinous substance of the bristles and of the claws?

[146]Le Dantec: Lamarckiens et Darwiniens. P. 142—145.
[147]Weismann: Neue Gedanken zur Vererbungsfrage. P. 65.

"I need not recall," continues our author, "the host of positive changes undergone by plants which cannot be explained by the Lamarckian theory,—the appropriately placed protective spines, bristles and hairs, the poisons, the tannins, the etherial oils of all kinds, and all the purposeful forms of leaves, of flowers and all parts of plants in general. In the case of all these the supposed inheritance of the effects of use and disuse in general does not come into question; in them everything proceeds without it,—an incontestable proof that nature does not require this supposed factor for its transformations." [148] It is probable on the contrary that many of these changes undergone in the past or in the characters now existing are rather simply the result of the reaction of the plant organs to a certain external or internal stimulus which has not yet been remarked nor indeed suspected. To this category belong very probably, for instance, all the various secretions of chemical substances. Further the very fact that secretions that are entirely alike occur in plant species that are quite unlike one another in everything else, speaks, as we shall see at once, in favor of the hypothesis that these same secretions are acquired and inherited characters. Other characters which likewise were formerly in all probability functional adaptations or are such now can incidentally serve other purposes and can therefore be useful to the species in other ways also, as we stated.

It is evident that Weismann, in order to support his assertion that natural selection is quite capable of explaining by itself the transformation of species, has allowed himself to be misled into denying arbitrarily

[148] Weismann: Neue Gedanken zur Vererbungsfrage. P. 66.

to a large number of modifications, which do not differ in their essence from the others, the character of functional adaptations. We would not deny that there are certain forms or structures, which, just because their functional character has not been perceived, have not heretofore received any explanation except through natural selection, even though it does not always furnish an altogether satisfactory explanation. But the deeper one goes into the essence of functional adaptation and the wider its field of action is seen to be, the number of these formations become less and less and with it dwindles away also this seeming almightiness to explain all physiologic transformations whatever, which Weismann would like to attribute to natural selection without producing proof for it.

3. The third argument based upon the neutral individuals of ants, bees and termites is well known as the chief question about which turned the polemic between Weismann and Spencer. The latter brought up as one of the strongest arguments in favor of inheritance, the co-adaptation, that is the co-ordinated modification of different parts co-operating to produce a definite physiological result. Weismann on the contrary sees in the existence of neutral individuals among the ants, termites and bees a refutation of Spencer's theory, since these individuals in the course of their phylogenetic development have undergone harmonious modifications of diverse parts, without ever having been capable of reproduction. To this Spencer replied that all the harmonious modifications of different parts, including the numerous instincts which the neutrals present to-day, are only the heritage of those which the ancestors of these now social insects acquired in a state of isolation or in a society in

which there was equality and in which there were no castes, the neutrals being nothing else than females incompletely developed because of defective nutrition.

It would not be correct to state that the question has been finally decided through this debate. While Weismann has not been able to prove conclusively that these harmonious modifications of the neutrals have been at least partially acquired after the development of castes and when the sterility of the neutrals had already appeared, neither has Spencer been able to demonstrate that all these harmonious modifications had been already acquired by the presocial ancestors. Nevertheless the conception of Spencer that the neutrals are produced by an arrest of development of the females has in our opinion won a decisive victory over that of his opponent, and has in reality taken from the last rampart of the Weismannists all the strength which it had derived from the conception that the neutrals were special formations, which had acquired special characters by fortuitous variations and natural selection only.

4. The fourth and last argument, that of the inconceivability of the transmission of acquired characters, has already been considered by Darwin in connection with examples which he had himself communicated of the inheritance of certain peculiarities, particularly of instincts acquired by domestic animals. "Nothing in the whole circuit of physiology," he stated in this connection, "is more wonderful. How can the use or disuse of a particular limb or of the brain affect a small aggregate of reproductive cells seated in a distant part of the body, in such a manner that the being developed from these cells inherits the characters of either one or both parents?

Even an imperfect answer to this question would be satisfactory." [149]

This argument which Weismann considered as the strongest, without indeed saying so definitely but allowing it to be seen, is in reality the feeblest of all. Even admitting that the mechanism of transmission may be at present quite inconceivable, that is no reason for believing that it does not exist, since the number of phenomena and even of natural laws which we must regard as certainly established, even though we cannot so far explain them in any way is, one can well say, infinite. It recalls the former objection to Newton's theory that it is inconceivable how the heavenly bodies could mutually attract one another at such a distance, and like this it is of no logical value. Apart from this it can have only one very important practical consequence, (and it has had this effect and as a matter of fact is still producing it), i. e. of bringing the reality of this inheritance into question with very many investigators and stimulating them therefore to a zealous search for a conclusive experiment which should once for all establish or exclude it.

In any case it is interesting to note that Nussbaum whose theory of the continuity of the germ cells suggested to Weismann his fundamental conception of the continuity of the germ plasm, is opposed to him in that he does not exclude the possibility of the transmission of acquired characters. For immediately after the exposition of his theory he states "since seeds and eggs are stored up in the parent organism, they are therefore subjected to the action of conditions which bring about

[149]Warwin: The Variation of Animals and Plants under Domestication. H. P. 367.

modifications of it, and so the transmission of acquired characters is not excluded." [150]

After thus having brought forward and refuted the four principal arguments adduced by Weismann against the Lamarckian theory, we must now examine the value of the corollaries and subsidiary theories which this investigator devised to defend his doctrine from the manifold objections which were brought forward from all sides to show its inadmissability.

Panmixia presents itself as the first subsidiary theory. It has entirely succumbed. It was devised by Weismann to explain the progressive phyletic atrophy of the organs which have become useless, and rests on the supposition that as soon as the fortuitous variation of a certain organ has become useless for the species, and is therefore withdrawn from natural selection, the minus variations which this organ would chance to present in certain individuals would no longer cause the disappearance of these latter in the struggle for existence. The survival of organisms with such minus variations and their sexual union with individuals which still preserve the organ in its original state would lead gradually to the degeneration, progressive atrophy and final disappearance of the organ.

Spencer, nevertheless, rightly draws attention to the fact that the appearance of plus variations is just as probable as that of minus variations, and therefore panmixia is not at all capable of explaining by itself this progressive and continuous degeneration of useless organs.

[150] Nußbaum: Zur Differenzierung des Geschlechts im Tierreich. Arch. f. mikr. Anat., Bd. 18. Erstes Heft. Bonn. Cohen. 1880. P. 113.

The addition suggested by Romanes that the tendency to atavistic reversion favors minus variations at the expense of plus variations, does not suffice.[151] For in the first place an atavistic reversion could appear at best only in the phyletic characters acquired last, and in the second place, after the first stages of atrophy had appeared it would in any case tend from that time on to insure the preponderance of plus over minus variations.

One could nevertheless assert that panmixia is not necessary for Weismann's theory. The principle of the economy of the organism by which every useless and unused organ is harmful because it withdraws nourishment from other organs is by itself enough, if one rejects the inheritance of acquired characters, to explain the gradual phyletic disappearance of useless parts.

But this hypothesis is easily refuted by some calculations of Spencer, showing that it is impossible that the advantage to the organism of a small inborn and fortuitous minus variation in the useless organ, particularly when this is already very much degenerated as is for instance the hind leg of the whale, can procure for the individual an advantage over others and so provoke the phylogenetic passage to a yet greater atrophy. And no great value can be attributed to the counter observation, which Weismann several times repeats, that we are still quite unable to measure the selective efficacy of the struggle for existence. One need think only of the parasites and particularly of the endoparasites, which have always an excess of nutrition and in which therefore the advantage of the degeneration of useless organs would become reduced absolutely to zero. And it is

[151]Romanes: A Note on Panmixia. Contemporary Review. October 1893. P. 612.

nevertheless in these that this reduction reaches its maximum.

However that may be, we might nevertheless admit either that, as panmixia supposes, fortuitous minus variations preponderate over plus variations, or that the principle of the economy of the organism is alone enough to secure the victory to those individuals whose useless organs are most atrophied. But, even in that case how could panmixia and the principle of economy in the organism explain the fact that the atrophic state of organs which have become useless, such as appears in adult organisms, results in the course of ontogeny from an involutive process of these organs which are better developed in the early stages than in the later stages? Although in so doing we anticipate a question which we shall examine again later in all its generality, we may note here that the most that panmixia and the principle of economy could do would be to explain the fact that the more recent a species with a given atrophied organ is, the earlier should be the stage of development at which the organ in question is arrested in ontogeny, whereas in the ancestral species it attained a greater development. But how can they explain how certain tissues and organs develop during ontogeny up to a certain and fairly advanced point and thereafter at a certain moment undergo a physiologic involution resulting in their degeneration and often in their complete disappearance?

As we pass on now from continuous, gradual atrophy of useless organs to the slowly progressive formation of useful organs and so to phyletic evolution in general, we must declare at the outset that of all the objections that have been urged and which can yet be urged against the

view that natural selection by itself is sufficient to account for the transformation of species, we shall bring forward only a very small number. For we believe it worth while to limit ourselves to the most characteristic and certain ones, which serve better than the others as an indirect support for the Lamarckian theory. And so much the more since in the case of many objections discussion is idle. For—and this may be said once for all—if our adversary adopts the complete sufficiency of natural selection both as his thesis and as the ground for the defense of this thesis, naturally it will be very difficult, indeed, often quite impossible for us to carry on the contest from a purely logical standpoint.

Candidly one could wish that Weismann would prove this omnipotence of natural selection by some facts. But he has still to furnish this proof. For, as we have seen, he has limited himself to showing that among the various hypotheses which have been devised to give account for certain special formations, natural selection is the one which fulfills this purpose relatively best.

But when once our adversary sets up this almightiness of natural selection as an axiom, to be employed at need as thesis or as the support of the thesis, it will then be very difficult, we repeat, in most cases to point out any contradiction in his tenets, which is the only means by which a logical refutation can proceed and reach any result. In other words, if in order to demonstrate the complete sufficiency of selection Weismann starts off with the supposition that natural selection is omnipotent, how can one by pure reasoning convict him of error?

And in fact: One investigator offers the objection that fortuitous variations even though they are useful

must nevertheless in many cases be so inconsiderable in amount, that they could not possibly constitute such an advantage as to give natural selection anything to act on. But Weismann in order to extricate himself from this embarassment needs only to repeat here again his habitual, axiomatic, already mentioned reply that we are unable to measure the degree of selective power of the struggle for existence.

Others object that certain characters due to functional adaptation are altogether useless to the species. One can conceive how they might be inborn in individuals if one admits the inheritance of acquired characters, whereas they would be quite inexplicable if one sought to ascribe them to natural selection alone. But Weismann has always the answer at hand that one cannot judge of their present or past usefulness. A typical example of these discussions which logical processes are powerless to decide is the question debated in the Spencer-Weismann polemic upon the especially acute taste sense of the tongue papillae. While Spencer attributes it to the continual rubbing of the tongue against the teeth and states that it is without utility for the organism; Weismann on the contrary asserts that it may have been of some use, at least in the past. We do not forget in this connection that the question might also be raised whether this fine sense of taste is really inborn or is not rather acquired anew in each individual after birth.

Others regard natural selection as powerless to bring about any transformation because the fortuitous variations or individual deviations, upon which it is able to act, are constantly destroyed by amphimixis. Weismann can always reply that the fortuitous variations or deviations preserved in an individual by natural selection are

not prevented from passing to descendants by the conjugation of this individual with others which do not possess any such variations, but are only diluted, so to speak. Therefore all that is necessary is to suppose the struggle for existence to be more severe or to have a higher degree of selective capacity than that which would have been sufficient if there had not been sexual reproduction.

It is well known further that Weismann, in order to afford natural selection abundant and never failing material upon which to act, has made for himself a weapon of sexual reproduction, attributing to it a great fruitfulness in the constant production of new variations. But he seems to have been partly converted finally to the opposite view of the Lamarckians already mentioned, that sexual reproduction only contributes to securing the unity and constancy of the species. For, in order to explain the production of a lot of fortuitous variations, he finally sought refuge in the unavoidable irregularities of nutrition in the germ plasm,[152] a thing which makes his hypothesis upon the biologic function of amphimixis quite superfluous. It may be merely noted here that when once one sees in amphimixis a cause tending toward the levelling of individual characters and consequently toward the fixity of the species, and thereby reducing by so much the probability that the selective capacity of the struggle for existence is alone sufficient, one must then feel so much the more strongly the necessity of discovering some cause of variation capable of acting simultaneously and in the same way upon at least quite a large part of the individuals of the species, and of

[152]Weismann: Das Keimplasma. P. 541—570.

acting also in this same direction throughout a decidedly large number of successive generations.

"One must admit," says Hartmann, very rightly, "that minute and purely accidental variations even if they are useful, are unable to preserve themselves from disappearing again through crossing. Whatever is to be preserved must, as Darwin also admits, appear in a certain quantity, either all at once or successively, because the number of similar variations must be sufficient to overcome the suppression through crossing. But it is not to be expected that similar variations will appear in such frequence by chance, but only as a result of definite external or internal causes which set a definitely directed modification in the place of accidental ones." [153]

Of the causes of variation which possess this capacity of simultaneous similar and constant action, we know at present only functional adaptation aided by the inheritance of acquired characters.

The very fixity of many species has been rightly urged against Weismann. Natural selection in fact, because of the smallness of fortuitous individual variations, is forced, on the one side in order to explain by itself the development of species, to fall back upon an excessively great degree of selective capacity; but on the other side if this great degree of selective capacity is accorded, it encounters still greater difficulty in accounting for the contrary phenomenon presented by a host of other species which have remained unaltered even during a whole series of long geologic periods.

The Lamarckian theory does not find any special

[153]Eduard von Hartmann: Die Abstammungslehre seit Darwin. Annalen der Naturphilosophie, herausg. v. W. Ostwald. Zw. Bd., Heft. III. Leipzig, May 26, 1903. P. 289.

difficulty in this. If the true provocation to alteration comes from the environment and not from natural selection, the evolution of certain species and the constancy of certain others may be explained simply by the respective alteration or stability of their environment.

The alteration of the environment could be brought about in the case of a given species not only through natural telluric changes but also for instance by the migration of this species toward other regions, or by the immigration of other species into its territory, often also by the overcrowding of its territory by the species itself.

Emigration as a cause of variation of environment does not need to be illustrated by examples.

The immigration of other species can immediately induce a very considerable modification of the environment. The immigration of a bird of prey with rapid flight will have as a result that the birds for instance of a certain native species are compelled to fly more rapidly in order to escape it. This repeated greater effort will develop an increase of their swiftness, an increase which would not have been attained, we must believe, by normal daily exercise. For the normal exercise of a given function after the respective organ has once been formed, does not develop it any further but merely causes it to preserve the degree of development already attained. In this way one can readily see also that if the region ravaged by the bird of prey is only one part of the whole territory inhabited by this aboriginal species, one portion only of that species will be forced to become transformed into a swifter variety while the remaining portion can and must remain unaltered.

The overcrowding of a given territory by a given

species can not only force this species to emigrate, or at least to widen its range of habitation, thus placing itself in contact with different telluric conditions and with different fauna and flora, but also it can itself induce directly very considerable modifications of the environment.

Thus, to take an already famous example, it is possible that the long neck and forelegs of the giraffe are to be ascribed to the overcrowding of the territory inhabited by its ancestors. For if we suppose that these ancestors at a definite time and in a definite region had become altogether too numerous in proportion to the trees present whose leaves served them for nourishment, then all the leaves up to a certain height would naturally have been eaten first, and there would finally remain only those leaves situated very high, so that in order to reach them the animal was forced to stretch out its neck with a greater effort than formerly and to stand upon its hind legs, falling later on the fore legs after plucking off the leaf. And these efforts so very different from the ordinary would have produced quite new morphological adaptations. But it is not at all necessary to suppose that all the individuals of this former species of giraffe were forced indiscriminately to this transformation. For many, perhaps becoming accustomed to another diet, could remain unaltered or undergo transformations of little importance.

In other cases, on the contrary, that part of the species which was driven through overcrowding of the territory to change its diet would be compelled to undergo the most considerable transformations. This would be the case, for example, when the overcrowding of a given tract of meadow land by a species feeding exclusively

on grass and herbs would force some of these animals to feed on tree leaves, others to become transformed into rodents and insectivors or to undergo some transformation of still another kind.

In this connection it is to be especially noted that just because a large number of the individuals of the old species will thus have come to seek their nourishment elsewhere, no change will appear in those remaining behind in the former conditions of nourishment. In other words the elimination caused by the change in their habits of the overcrowding individuals from among the company of the old species will leave the other individuals of this species, whose number will now be no longer too great, in the same conditions of environment as formerly, without any overcrowding and consequently there will not be any further causes provoking in these individuals also a transformation into another species.

The change of nutrition will induce then a whole series of changes in the functions of seeking food, hunting, fighting, seizing, chewing etc., but only for that position of the species which has changed its mode of living. Thus it is clear how, during a series of entire geological periods, a certain number of the ancestors of individual species that are now quite different from them were able to preserve themselves unaltered and so to reproduce their descendants unaltered to this day.

Man is distinguished from other animals perhaps in this, that whereas the latter do not modify their environment or modify it only indirectly and intermittently by emigration or by overcrowding and consequently make no progress in their development so long as their environment undergoes no alteration from one of the causes

mentioned or from some other accidental cause, man on the contrary modifies his environment directly and continuously by the products of civilization. And this unceasing modification of the environment results in the unceasing evolution of the man.

It is thus for example with cerebral development. Civilization itself and the continual progress of science and arts make steadily increasing demands upon the brain. And this mental exercise, steadily increasing from generation to generation, contributes always to the development of the brain. What wonder then, if the cranial capacity of man has become markedly increased even during the three last centuries, as is stated by the anthropologists?

Another cause whereby one portion of a given species can remain unaltered while the remaining portion becomes transformed, is found, when once the inheritability of acquired characters is admitted, in the sudden apparition of certain instincts. "Also in the domain of biology," writes Emery, "and very especially in that domain, many characters of organisms seem to me to permit of explanation only by sudden formation. This is especially true of habits and instincts. How could the first Velleius dilatatus arrive gradually at its parasitic life in the nest of the hornet? The first cuckoo certainly commenced suddenly to deposit its eggs in the nest of a strange bird." [154]

The first sudden appearing of a new instinct can be compared to a happy thought. It is a definite association of ideas which is formed for the first time. But when it has once been formed, it is easily possible and indeed

[154] Emery: Gedanken zur Deszendenz und Vererbungstheorie. Biol., Centralbl., July 15, 1893. P. 416.

probable that it will be formed often again in the same individual, and this repetition will produce a constantly increasing, corresponding modification of the nervous tissue in the individual concerned, which will be reproduced in his descendants. A new association of ideas can arise and actually does arise independently, within certain limits, of the nervous structure of the individual, and therefore independently of the germ substance also which has produced this latter, in so far as the fortuitous external circumstances which produce this new association exert a strong and overmastering influence: Among a thousand individuals, quite identical in regard to the structure of their nervous mechanism, this new association of ideas will be developed in only one, on account of the special external circumstances in which it happens to be placed.

But without the inheritance of acquired characters this fortunate new association of ideas, and the repeated employment of it by the individual later, would be completely lost for the species. To assure its transmission from one generation to another there would remain only imitation or education in the widest sense of the word. But the fact is that nearly all the instincts are, on the contrary, truly inborn, that is to say they are produced without any psychic educative influence whatever.

It is clear also that not all the members of the older species will be able to make use of a new, fortuitously developed instinct through educative imitation and later through heredity, but only the immediate descendants or associates of the individual in whom it was developed. All other members of the species would be excluded. And so those will be the only ones, who, in consequence of this newly adopted habit, will make a thorough

change in their former manner of life, and in whom consequently the whole organism will be modified through functional adaptation. In this way may be explained the transformation of only one group of the individuals constituting a species into a new species, while the others remain unchanged.

These few examples, even though so briefly outlined, are nevertheless quite enough to show us that the Lamarckian theory is capable of explaining at the same time both the evolution and the fixity of a species. But how can Weismann account for the inalterability and constancy of a given species? It goes without saying that he has no hesitation in attributing it, like variation itself, to natural selection again. But even if one were willing to suppose the environment immutable, is it possible that any species could ever come to such a degree of perfection in relation to its environment that every new variation in any direction whatever must make the conditions of this species worse and make its members less likely to be victorious in the struggle for existence? Is it not much more probable that however high a degree of adaptation to its environment a species may have attained, it can always become even better equipped for the struggle for existence through further transformations in certain directions, and consequently offer still greater opportunities for natural selection which is everywhere and always upon the *qui vive?*

We must nevertheless be careful, in relation to this question of the fixity of species, not to attribute to the arguments which we have just set forth any greater value than they actually possess, especially because we know nothing, or only a very little, concerning the immediate circumstances that have actually existed in the develop-

ment of even a single species, and still less, if that is possible, concerning the true mode of procedure of this natural selection which is so difficult to control. So that we must content ourselves with putting forward the views which we have just outlined merely as further conjectures speaking in favor of the Lamarckian theory, without seeking to attribute to them the value of logical proof.

Structural relations in general and the most remarkable ones in particular, such as the static structure of bone, of certain tendons, of certain membranes, the dynamic structure of the smooth and striated muscle tissues and other similar formations, which represent the most perfect functional adaptation and the best utilization of the material down to the minutest and most delicate details, testify likewise in favor of the transmissibility of acquired characters. "All these formations of connective tissue, muscle and bone," writes Roux, "could never have been developed in such regularity and completeness by Darwinian selection from individual variations of form, since here there must necessarily have been thousands of fibers and cellules already accidentally arranged in this purposeful fashion in order to produce even the smallest advantage appreciable in the economy and capable of being acted upon by natural selection, and so much the more since in the extremity of hunger these would be exactly the parts, the heart excepted, which, thanks to the small amount of metabolism in them, would suffer last of all,—much later than other more vitally important organs with more active metabolism. These formations could not therefore arise from the selection of individual variations in form, but are rather derived only from those qualities of the respective tissues

to which is directly due the fashioning of the adaptation even to the smallest details." [155]

But Weismann could very lightly deny to these very perfect structural formations any value as even indirect proof of the principle of inheritance. From his point of view he needs only to object that since they are useful to the species they can then be very easily explained by natural selection alone, and no refutation would be possible.

Inborn characters have the tendency to become like those which the ancestors acquired by functional adaptation, and this coincidence speaks also in favor of the hypothesis of the inheritance of acquired characters. But against this also Weismann would have no lack of words and apparent arguments.

Functional adaptation, he could reply, renders the species more capable of resistance. The greater the individual disposition to this adaptation the more rapidly the adaptation will proceed. Consequently those individuals upon which this disposition is especially impressed will survive, and above all those individuals in which this adaptation is already existent potentially in their germ plasm. Thus the coincidence in question could be explained without requiring the adoption of the inheritance of acquired characters.

In this way one would arrive at the conclusion that all characters susceptible of being produced by the innumerable functional adaptations must for that very reason be always useful to the species, so that they can be fixed even when they happen to be actually produced by fortuitous inborn variation. We shall not consider this further

[155]Roux: Der Kampf der Teile im Organismus. P. 30.

for it would lead us back to the question which Spencer has raised with his example of the more acute sense of taste in the papillae of the tongue, and of which we have spoken above. But apart from that, is it possible for this argument, however unassailable it may be from a purely logical point of view, really to weaken the strong presumption in favor of transmissibility which is derived from the fact that inborn structural relations always follow—though slowly and tardily—those acquired in life through functional adaptation, as the shadow follows the body?

Another fact among those which speak most convincingly in favor of the inheritance of acquired characters is the similarity of certain structures in different species which are subjected to the action of the same mechanical conditions. Without needing to bring up the most typical and most familiar case, viz., the transformation of the extremities of the whale into fins, it would be enough to recall as examples the like character of the leg joints in the two-hoofed animals (Diplartha, Cope) and the rodents, which is attributed to their rapid locomotion; the like structure of the extremity of the radius in the edentates and the quadrumana which possess the power of supinating the hand; the like reduction in number of the digits in many orders of digitigrade mammals which run about on the dry hard ground; the like modifications in the form and development of crests on the skull following like employment of the canine teeth as fighting teeth in all orders in which these teeth are strongly developed.[156]

[156]Cope: The mechanical Causes of the Development of the hard Parts of the Mammalia. Journal of Morphology, vol. VIII, No. 2. Boston, U. S. A., Ginn, Sept. 1899. P. 159—163, 164—165, 175—176, 182—183, 201—203, 273.

For if these structures had all arisen through natural selection only, selecting the most fit from among all the chance variations, one could not explain how, in different species, even though they were subjected in respect to that particular organ to like mechanical conditions, it could lead to one and the same result. In fact how could one affirm that the structure of any given organ must be of one certain character only and no other, in order to render the species most fit for the struggle for existence? So mere chance must be invoked to account for the fact that of the numerous structures among which natural selection could choose, it has selected in the most different species subjected to the action of the same mechanical conditions in relation to only one of their organs, just one single structure for this organ, absolutely alike for all these different species.

A similar phenomenon, which leads one toward the same view, is mentioned by DeVries, as already noted, in support of his theory of pangens or preformistic germs, representative of definite characters; namely, that the most diverse species of plants have often the power of producing a greater or less number of identical chemical compounds. "Insectivorous plants, for example, belong to the most different natural families, nevertheless they all possess the faculty of producing from their leaves the necessary mixture of an enzyme and an acid requisite for dissolving albuminous bodies." [157] Darwin himself has already remarked that this mixture is quite similar to the gastric juice of the higher animals.

Now without wishing to touch anew upon the question of preformistic germs which we have already dis-

[157] De Vries: Intracellulare Pangenesis. P. 8—10.

cussed, it may merely be remarked here that the existence of these like properties, acquired in the most different species, is easier to explain by the Lamarckian theory than by natural selection. For just as substances exposed, for example, to identical calorific influences finally all take on the same degree of temperature, and yet all remain quite different from one another in other characters, so when quite different species are exposed, on account of the environment, or nourishment, or peculiar conditions of light, or of any other cause whatever, to functional stimuli which incite them, for example, to secrete tannic acids or alkaloids, and so on, these secretions, acquired by means of functional adaptation and transmitted later by heredity, must come to be present in several species, even though all other characters can remain different.

Here it seems to us, there remains for Weismann nothing else than to affirm that these like characters may have been fixed by natural selection in the most different species because, from the likeness of the functional stimuli to which, according to the hypothesis, these species were exposed, the same characters must have been the most useful for every one without exception. But this must first be proved. And so much the more since in this case it is more difficult than in other cases to see the absolute necessity that all characters or peculiarities whatever, which are due to the reaction of the organism to the most different external influences and often to insignificant ones, must always be useful to the individual, and that therefore they must also possess this utility even when they are produced rather by means of inborn fortuitous variations.

If the soundness of this conception, required by the

theory of Weismann, of the selective utility of every inborn character which happens to be a repetition of a functional adaptation induced by reaction to any external influence whatever, is very doubtful, and in any case far from having yet been proved; yet the utility of one part of these acquired characters is proven and indubitably established. And indeed it is just from this utility that one of the strongest arguments against the presumed non-inheritance of acquired characters is derived.

Since in fact the usefulness of some functional adaptations to the individual is great and sometimes extremely great, it must immediately follow from that, according to Weismann's view, that the inheritance of acquired characters is itself the result of natural selection. For the species in which this inheritance began to manifest itself even though to a slight extent would certainly have had an advantage over the others, just because the adaptation to the environment in their descendants could go on with ever increasing rapidity.

"As modifications acquired by use during life," writes Cope, "are necessarily useful, it follows that if one accepts the post-Darwinian or Weismannian theory the only mode of acquisition of useful variations which we know is excluded from the process of organic development."

"Each generation should commence, in the matter of useful characters acquired by use, at the same point at which its ancestors had commenced, so that an accumulation or development of these characters would hardly be possible. The influence of the environment as well as the energies of the living being would be incapable of developing in a given generation more than only that which this generation could acquire during its single life. How could evolution, then, account for the law, which

paleontology has demonstrated in so splendid a manner, of the gradual modification of certain parts through long geologic ages toward ideals of mechanical perfection, for example, of the gradual perfecting of the skeletal articulations? Not only does the post-Darwinian school afford no explanation of this but with the acceptance of its theories this progress is indeed impossible." [158]

And Osborn's view is similar. "Living matter," writes he, "is characterized by a capacity of adaptive or purposeful reaction. If this capacity is inherited in the Protozoa, thanks to the simplicity of their process of propagation, it must be the same in the Metazoa. For each newly developed metazoon which retains the advantage of the inheritance of the adaptive reaction would be preserved, while each individual which loses this would degenerate. The mechanism of the inheritance of ontogenic adaptation must then have been developed in passing from the unicellular to the pluricellular forms by means of natural selection." [159]

Weismann it seems to us could reply only by saying that natural selection may not have established the inheritance of acquired characters in the pluricellular forms also, because the production of the mechanism necessary for that purpose had become materially impossible by reason of the structure of the metazoic organism. But this assertion, which would limit the capacities of living organic substance, must appear a little too hazard-

[158]Cope: The mechanical Causes of the Development of the hard Parts of the Mammalia. Journ. of Marph., vol. VIII, No. 2, Boston, U. S. A. Ginn, Sept. 1889. P. 140—141.

[159]Osborn: Alte und neue Probleme der Phylogenese. Ergebnisse der Anatomie und Entwicklungsgeschichte, herausgegeben von Merkel und Bonnet. Band. III. 1893. Wiesbaden, Bergmann, 1894, P. 607.

ous and quite unfounded, especially when one thinks that apart from that there is no process or phenomenon in the organic world which Weismann does not ascribe to the almightiness of natural selection. Thus the power of regeneration, sexual reproduction, the physiological necessity of death in the pluricellular forms, all are based upon natural selection. And is the almightiness of natural selection insufficient only for the inheritance of acquired characters?

After bringing to a close this rapid review of the objections which Weismann can always oppose to any argument, thus enabling him to save himself from complete defeat at least with the help of mere words and with a semblance of logic, it remains for us, before passing to the following chapter, to examine two other objections to his views which seem to us particularly important, in that the arguments which he opposes to them appear to involve his own theory in the most striking contradictions. These are the inexplicability of coordinated variations, and the repetition of phylogeny by ontogeny, and with these we shall close the present chapter.

The objection to the conception of the complete sufficiency of natural selection which arises from coordinated variations is well known. When the utility of certain modifications of the organism depends upon the correlative development of many quite different parts natural selection cannot account for the interdependent, phylogenetic modifications, since, for the production of these latter, it can act at best only upon special fortuitous variations which are independent of others and from that very fact totally useless.

Roux for example describes in a masterly way the

contemporaneous formation of thousands and millions of new characters each adapted to the others and all combined to perform some function such as must be necessary in the phylogenetic passage from an aquatic to a terrestrial life. And he concludes in these words: "One must necessarily conclude that functional adaptation, such as is produced in alteration of the conditions of life, can bring about purposeful co-ordinations simultaneously in all organs of the body concerned. And the characteristic feature of this simultaneity of action in millions of parts must be the fact that it is opposed to the action of natural selection which can never develop simultaneously more than a very limited number of purposeful characters." [160]

Weismann on whom the force of this objection arising from correlative development is not lost, has sought to get around the difficulty by setting over against it, as we have noted above, the neuter forms in bees, ants, and termites. He does not deny the extraordinary difficulty of explaining co-ordinated variations by natural selection, but expects to show that in spite of it there exist undoubted examples in which this difficulty was overcome by natural selection.

As to the polemic which raged between Weismann and Spencer on the subject of these neuters, we have already seen how in our view Spencer has succeeded in driving his opponent from any tenable ground by demonstrating convincingly that the neuters are really nothing else than incompletely developed females. We shall not return here to what has already been said.

But it is worth while to observe that Weismann thus

[160]Roux: Der Kampf der Teile im Organismus. P. 39—44.

deprived of his last stronghold saw himself forced to give an explanation for these co-ordinated variations also, which should prove, at least from a theoretical point of view, that they also might possibly be produced through natural selection. But it is just in this attempted explanation that he has fallen into the most evident contradiction, a thing which was inevitable anyway seeing that his thesis is untenable. It is worth while to spend a little more time examining this contradiction.

He utilizes for this purpose a theory which, though introduced only at the last to supplement or replace the earlier, already discussed theories of panmyxia and the economy of the organism, was originally intended to give if possible some better explanation than the earlier theories offered of the continuous regression of useless organs even after any further regression is of no more value for natural selection. According to this theory when once the involutive process has begun in a given organ from any external provocation whatever, it would acquire in this very way an intrinsic tendency to bring about more and more retrogression. And the tendency acquired by this organ and now inherent in it toward constant phylogenetic regression would be accounted for by the following consideration.

Weismann affirms that when the tendency to degenerate once appears in an organ especially well developed, let us suppose by natural selection, that proves that it is represented from that time on in the germ plasm by determinants "of smaller growing power." "But since," he continues, "growth and assimilation are physiologic functions, just as are contraction and secretion, so the fundamental principle of intraselection is applicable to them: the functional stimulus strengthens the function-

ing organ, and the part which performs its function more energetically attracts to itself more nutrition and repairs with interest its loss of matter more rapidly than does the part performing its function less energetically. So in the struggle of the parts for nutrition the more feeble determinants will be at a disadvantage, they become slowly but constantly feebler in the course of generations until finally they degenerate completely." [161]

So that according to the view of this investigator: "It is not the functional change that is inherited; but variations in the biologic value of a part, (for example, of an organ which has become useless), give the impulse to the regressive or progressive variations of the germ plasm and these only would establish the hereditary functional change of the somatic part." [162]

Now it is just this conception of determinants "of smaller growing power" which is quite inadmissible, and which constitutes a contradiction in terms.

For what signifies in general "weaker" or "stronger" determinants? The determinants of a small organ are by their very definition not feebler than those of a larger organ; they are only qualitatively different from them. Also when the variation of an organ consists in a diminution of its mass, this is not a diminution of growing power of the respective determinants but an alteration of these latter, which is nothing else than their replacement by other qualitatively different determinants. Would Weismann himself say that the respective determinants of the fore legs of the kangaroo are provided with a smaller power of growth than those of the hind legs? Or that the fingers of the human hand have determinants

[161] Weismann: Neue Gedanke nzur Vererbungsfrage. P. 14—15.
[162] Weismann: Ibid. P. 59.

whose power of growth stands in exact proportion with their length? Would the shorter fingers therefore have a phylogenetic tendency to become constantly still shorter, and the longer fingers a tendency to become steadily longer yet? If that were so it would lead directly into this absurdity, that the formation in phylogeny of new organs or of new structures in general could never have any commencement, since originally their determinants, just because of the very smallness of these formations, must have been provided with only a very small power of growth and therefore could never progress side by side with determinants which must in any case be stronger since they belong to organs or structures already developed.

If on the contrary this is not the case and cannot be the case because it contains an unavoidable contradiction, then the determinants of any degenerated organ whatever, such for example as the hind leg of the immediate ancestor of the whale, cannot be regarded as feebler, but must rather be regarded as qualitatively different from those of the complete organ. Consequently there cannot exist for the degenerated organ any phylogenetic tendency to become still more rudimentary.

Weismann would give, as we have said, a quite similar explanation of co-ordinated variations:

If there were, for example an increase of the weight of the head, as a direct result let us suppose of natural selection, certain muscles of the body after having received an initial impulse from natural selection itself, would acquire a phylogenetic tendency to grow *pari passu* with the weight of the head. For the first operation of natural selection would be to eliminate individuals whose muscles were too feeble. Then even if we suppose that

every fortuitous variation that is possible, both plus and minus, actually develops, the net result after the elimination of the minus variations must be that the muscles would be stronger. But this initial increase, this first impulse toward strengthening, would be in turn the cause of a phylogenetic tendency to a further strengthening, because it would indicate that these muscles were represented in the germ plasm by determinants which are endowed with a greater power of growth, and consequently with greater power of assimilation. "The affluence of nutritive fluids would become proportionally augmented and would contribute likewise to giving the plus variations a preponderance over minus variations. There would thus be a phylogenetic tendency toward the continual increase of these muscles and it would endure just as long as the increase in the weight of the head, and would stop when the latter stopped. For in this case the plus variations of the determinants would be eliminated by individual selection, as soon as they attained selectable value." [163]

But this artificially constructed hypothesis, which did not hold good at all in the case of rudimentary organs, is still less adapted to the case of co-ordinated variations. For in these phenomena it appears still more clearly that in phylogenetic changes there are concerned not simply exclusively plus or minus variations, but transformations which might be constituted by a combination of increases in one direction and decreases in another, or might not be susceptible of being decomposed into merely quantitative variations. It should be noted further that for certain correlative, histological varia-

[163] Weismann: Neue Gedanken zur Vererbungsfrage. P. 22.

tions of physico-chemical nature, which are concerned in any way in the fundamental specific characters of vital processes, the expressions increase and decrease have no significance at all.

Nevertheless it would not have been advisable not to mention here these later explanations of the atrophy of organs which have become useless and of co-ordinated variations, because the fact that Weismann substituted them for his earlier ones, shows that he himself regarded the earlier explanations as insufficient, and because the artificiality of these new explanations shows very clearly the almost insurmountable difficulty encountered in the attempt to explain these phylogenetic phenomena if the inheritance of acquired characters is rejected.

But the phenomenon which more than any other remains an enigma when the inheritance of acquired characters is rejected, and which when this inheritance is accepted becomes not only self explanatory, but sets the whole mechanism of inheritance in the clearest light, is that of the repetition of phylogeny by ontogeny, and just because of this we reserved it for the last.

"Whenever a new species is formed," writes Delage, "it is accomplished by the addition of one or more new characters, at the end of ontogeny, after all the old specific characters have already appeared. And since this goes on from the very commencement it is evident that the characters must appear in ontogeny, in the same sequence as in their phylogenetic formation." [164]

But if there is no inheritance of acquired characters why should the new character be invariably just *added* to those already present, and *only after* the development of the latter is completed? Why should it not be possible

[164] Delage: L'hérédité etc. P. 366.

for each variation of the germ substance to appear or to become active, either from the beginning, or at any time at all during the ontogeny?

"The phenomena of latency" says Osborn, "speak absolutely against Weismann's conception, according to which phylogenetic development would take place in the germ plasm by selection of advantageous elements, and elimination of disadvantageous elements. These phenomena of latency indicate that the phylogenetic process does not consist in an elimination but in a shoving of certain characters into the background (Zurickdrängung) during the later stages of ontogeny."

Osborn cites as example the well known experiments of Cunningham on the color of the asymmetrical flat fishes, pleuronectids, on whose lower colorless side artificial illumination is followed by a reappearance of the pigment disposed in the same designs and in the same colors as on the upper side, and also Agassiz's experiments according to which the young of these same fishes retain their original symmetry when they are kept at the surface of the water for a longer time than under normal conditions. "According to these experiments," Osborn says very rightly, "progressive inheritance (and so phylogeny) appears to represent rather a process of substitution or of addition than one of true elimination in Weismann's sense." [165] Thus these facts also speak in favor of the conception that phylogeny rests upon an addition of new characters and their superimposition upon the old.

We can see that to explain by the inheritance of acquired characters this addition of a new character to the

[165]Osborn: Alte und neue Probleme der Phylogenese. Ergebn. d. Anat. u Entwicklungsgesch., herausg. v. Merkel u. Bonnet. Bd. III. 1893. Weisbaden, Bergmann, 1894. P. 610, 619.

old only after the completion of the development of these latter, it is sufficient to suppose that the agent of transmission of an acquired character becomes active in ontogeny, only when the young organism finds itself in the same conditions in which the parent organism was when it acquired this character.

As soon as one admits this condition for the mechanism of inheritance the law of the repetition of phylogeny by ontogeny appears to be merely the immediate consequence of the inheritance of acquired characters.

For so long as the embryo is developing in the egg or in the maternal body and so long as it is nourished, supported and protected by its parents, it is withdrawn from the changing influences of the environment. It is only when the individual is left to himself that he finds himself driven perhaps to new functional adaptations. In other words it is only in the adult state, after it has completed or almost completed its specific development, that the organism in general can find itself in conditions necessary for the acquisition of new characters.

But another fact also can explain why new phylogenetic characters are acquired only when all the old ones are already quite developed. We have indeed already seen that the organism undergoing development is much more elastic but much less plastic than the adult, so that the modifications which arise in it from the action of an external force, even when it acts for a long time, have the tendency to disappear without leaving any trace behind so long as the organism has not yet completed its development, whereas this tendency is no longer inherent in the adult organism.

We have already mentioned the experiment of Roux, in which he distorted a few frog embryos within their

gelatinous envelope by compressing them between needles: "If the needles were withdrawn again immediately after the deformation, the embryo at once resumed its earlier form. If on the contrary they were held in place for several hours the deformation became from the first a persistent one, and only after several hours would the embryos resume their original form—a proof that an internal adaptation to the new form had already commenced, but that this adaptation is nevertheless caused to disappear again in the course of further development, perhaps by the action of those very forces of growth which bring about the restoration of the normal form, and which were inhibited during the time of the deformation." [166]

We have thought it worth while to mention again this very characteristic example of the elasticity of development, because it, better than others which we have already mentioned in the course of our investigation of the cause of this elasticity, helps us to explain the rule inviolably followed in the evolution of species, of the addition of new phylogenetic characters to those already present. For from this it is very evident that those phylogenetic characters whose appearance is caused during ontogeny to some extent by the action of external influences, have the tendency to disappear again promptly as soon as the cause which produced them has ceased to act. So that, unless we have an extraordinary influence, whose intensity and insistent action during ontogeny through the course of successive generations give it an

[166] Roux: Zur Orientierung über einige Probleme der embryonalen Entwicklung. Zeitschr. f. Biol.; Bd. XXI. München. July 1885. P. 515, 516. Gesamm. Abhandl. II. P. 245.

overmastering power, it will not leave behind any trace in the individual and certainly none in the species.

Thus the inheritance of acquired characters, thanks to these two facts that the embryo is usually withdrawn from the influence of the environment, and that organisms undergoing development are elastic and not plastic, shows itself to be completely capable of accounting for the fundamental biogenetic law. Whatever in it could seem marvelous and enigmatic finds its natural soultion and the law itself becomes an immediate and necessary consequence of this inheritance.

What on the contrary is the explanation which Weismann is able to give for this law? He thinks to explain it merely by the following laconic words:

"The biogenetic law rests upon this, that phylogenetic development is accomplished partly by the addition of new ontogenetic stages at the end of ontogeny. In order that this latter may be attained, the preceding terminal stages must each time be run through again."[167]

But in this Weismann leaves just the most important part of the question out of consideration. Why can phylogenetic development take place *only by the addition of new ontogenetic stages at the end of ontogeny?*

According to Weismann's theory, there is no reason whatever why one should believe the determinants corresponding to the last ontogenetic stage to be the only ones to undergo modifications, for one cannot forget that according to this theory each cell of each ontogenetic stage must have its own determinants.[168] The same causes of differences in the nutrition or any other thing, which are capable of modifying the determinants cor-

[167]Weismann: Das Keimplasma. P. 110.

[168]Weismann: Ibid., e. g. P. 97, 100, 232—233, 596.

responding to the last ontogenetic stage, must be also capable of transforming in the most different ways the determinants of the other stages. According to that, each phylogenetic stage would have its own ontogeny, which would differ completely even in the first stages of development from the ontogeneses of the preceding phyletic stages.

And there is no more reason for the supposition that the only way in which the determinants corresponding to the last ontogenetic stage could undergo modification must be by "obtaining a greater power of growth, augmenting consequently in number, differentiating each in a new fashion, and adding thus at the end of the old ontogeny one or more generations of cells."[169] For these determinants could perhaps undergo any merely qualitative variation whatever without first augmenting in number, that is to say could become differentiated at once in a new way so that the part determined by them should at once take on a form different from the old one without needing first to pass through its preceding phylogenetic state.

We need just to recall again the example which we have already cited above, furnished by one of the most characteristic manifestations of the fundamental biogenetic law, namely ontogenetic involution, in order to demonstrate in the clearest way the absolute inability of Weismann's theory, to account for that law. For according to that theory one would understand for instance that the tail of the ancestor of the tadpole, or that the limbs of the ancestor of the existing serpent may have become constantly shorter in the course of phylogeny by virtue of

[169]Weismann: Ibid. P. 110.

natural selection, panmixia or something else, and that consequently they have become arrested in successive ontogeneses at successively earlier stages of development. But the question cannot be repeated often enough; how can this theory explain the growth of these organs up to a certain stage of development and their retrogression and disappearance in the later stages?

In short, it seems to us that one cannot imagine a more complete overthrow even from a purely logical point of view, where it is only a matter of avoiding contradiction on one's own premises, than that suffered by Weismann in the attempt to find an explanation of the repetition of phylogeny by ontogeny, and one can hardly bring forward a more thorough failure of a theory built up laboriously with the object of explaining all the different phenomena of heredity, even the most peculiar and secondary ones, than appears in the fact that this theory is not even capable of giving the least explanation of the most general biogenetic phenomenon—the one which underlies all the others. And this contradiction and this failure do not appear so much in the minute and particular parts of Weismann's theory, in which it deals with this or that peculiar detail, but much rather in the theory itself in all its generality, which disputes the inheritance of acquired characters. Weismann and his supporters can, if the most evident facts are not enough for them, deny this law of recapitulation. But that they admit it and nevertheless dispute inheritance, this is a contradiction from which the opponents of the Lamarckian principle cannot escape now or ever—a destructive rock upon which all their theories are wrecked.

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If now we sum up succinctly the discussion in this

chapter, we are able to affirm that although no fact or argument is capable by itself alone of affording an irrefutable and unconditional proof either direct or indirect, of the inheritance of acquired characters, nevertheless the sum total of the facts and the arguments which are favorable to it is so weighty that one is not only justified in believing but is even compelled to believe that the Lamarckian principle is in all probability correct.

But the difficulties of explaining the mechanism of inheritance are so great, that many investigators may have thought them to be insurmountable. It is conceivable that many others, like Roux, have been led to dispute its existence, just in order to free themselves in that way from a veritable nightmare. But this position is no longer possible.

The objective examination of the question leads to the conviction that the inheritance of acquired characters is to be considered as in all probability a reality, therefore we are in duty bound to seek an explanation of this phenomenon by some hypothesis, even if it be only a provisional one.

So in the following chapter we propose to examine comparatively a few of the most recent and most important hypotheses which have been devised for the explanation of inheritance. After that in the penultimate chapter we shall set forth more thoroughly the explanation of the Lamarckian principle which the centro-epigenetic hypothesis can give.

Further evidence that somatic changes induced in animals by environmental influences may be repeated in their descendants as a result of germinal influences is furnished by Sumner and by Kammerer. See Archiv für Entwicklungs—Mechanik der Organismen, Leipzig, June and September, 1910. (Translator.)

CHAPTER SIX

THE MOST IMPORTANT OF THE EXISTING BIOGENETIC THEORIES IN RELATION TO THE INHERITANCE OF ACQUIRED CHARACTERS.

We believe it is unnecessary to discuss here in an exhaustive way the fact that the question of the admissibility or inadmissibility of the Lamarckian principle remains always distinct from, and entirely independent of the question of the evolutionary or epigenetic nature of development. Darwin in his evolutionary theory with preformistic germs,—a true theory of preformation,—accepts inheritance; Galton limits it to a few cases; Weismann excludes it unconditionally. Hertwig accepts it in his epigenetic theory, although he does not exclude some sort of preformistic germs; DeVries excludes it. Roux who was inclined at first to believe that this inheritance might exist in combination with the chemical development of the egg, a theory frankly evolutionary without preformistic germs, has finally regarded the two theories as irreconcilable. The only theories which appear especially inclined toward the complete acceptance of the Lamarckian conception, are the epigenetic theories without preformistic germs, for example that of Spencer.

We can now pass on to the rapid review of the principal biogenetic theories current today, with especial reference to their direct or indirect relation to the ques-

tion of inheritance and to the conceptions of inheritance which have been formed.

Spencer

This author's idea of "physiological units," intermediate between the morphological units or cells and the chemical units or molecules, and representing the last irreducible vital elements, is well known.[170]

If one supposes that in each organism there exists only a single variety of these units, Spencer believes the explanation of the inheritance of acquired characters would follow immediately from that.

"Just as the physiological units because of their special polarities build themselves into an organism of a special structure, so on the other hand, if the structure of this organism is modified by modified function, it will impress some corresponding modification upon the structure and polarities of its units. The units and the aggregate must act and react on each other. If nothing prevents, the units will mould the aggregate into a form which will be in equilibrium with their pre-existing polarities. If contrariwise the aggregate is made by incident actions to take a new form, its forces must tend to mould the units into harmony with this new form. And to say that the physiological units are in any degree so moulded as to bring their polar forces towards equilibrium with the forces of the modified aggregate, is to say that when separated in the shape of reproductive centers, these units will tend to build themselves up into an aggregate modified in the same direction." [171]

[170]Spencer: Principles of Biology, Sixth edition; London, Williams and Norgate. 1898. Vol. I. Chap. IV, § 66. P. 224—226.

[171]Spencer: Ibid. Vol. I. Chap. VIII: Heredity, § 84. P. 319.

It seems to us quite superfluous to expose any further here the pure verbality of such an explanation without any real content. Neither shall we go more closely into the objection, which is apparent on the very surface, that physiological units identical throughout the whole organism cannot form muscles here, bones there, nerves elsewhere, all of which represent special tissues with totally different physical, chemical and vital properties.

We limit ourselves rather to noting that, according to this, the inheritability of even quantitative and partial modifications, for example the transmission of the merely greater development of a tissue or an organ already existing, must be attributed to a uniform, qualitative change of all the physiologic units of the organism. And notwithstanding that, the properties of each group of these units, not excepting the group constituting the tissue which has undergone a simple increase in mass, must remain identically the same as they were before.

Let us consider the case which Spencer himself quotes and regards as one of the examples of the inheritance of acquired characters, namely, the increase in size or greater development of the great toe as well as the diminution or regression of the little toe, as a result of the fact that our ape-like ancestors gave up life in the trees for life on the surface of the ground.[172]

Is it possible that so very local a morphologic change has transformed qualitatively the physiological units of the entire organism? And apart from the fact that the change is limited to a certain very small part of the body, it must yet be borne in mind that one has to do here with no new quality nor with any new material introduced

[172]Spencer: A Rejoinder to Prof. Weismann. London, Williams and Norgate. 1893. P. 3ff.

into the organism by the new function, nor consequently with any new physical or chemical or biological character which the organism has now for the first time acquired; but on the contrary there is involved only a *different distribution of already existing qualities of matter.* But how can a change of quality in imaginary physiological units, which would have proceeded uniformly in the whole organism, accord with the fact that all the qualities and properties of this organism remain unaltered, and there is merely another distribution of these materials?

Let us consider as a further example the instinct of new born chickens. "In the first minutes of life," writes Jastrow, "chickens follow with their eyes the movements of crawling insects, turning their heads with the precision of an old fowl. In from two to fifteen minutes they pecked at some speck or insect, showing not merely an instinctive perception of distance but an original ability to judge, to measure distance with something like infallible accuracy. A chicken hooded as it emerged from the shell was unhooded when three days old; six minutes later it followed with its head and eyes the movements of a fly twelve inches distant, and about ten minutes later made a vigorous dart at the fly, seized and swallowed it at the first stroke." [173]

Spencer would rightly attribute this instinct to the long practice acquired by the ancestors of the chicken. But if he wished to explain this inheritance through the alteration of specific physiological units of the entire organism, such an explanation would not be taken seriously. How could the new physiologic units, capable of effecting this local modification constituted by the

[173]Jastrow: The Problems of Comparative Psychology. The Popular Science Monthly. New-York. Nov. 1892. P. 36—37.

formation of a few new nerve paths, at the same time reproduce those parts of the organism which remained entirely unaffected by this local change?

Finally, how can the hypothesis of Spencer account for the law of repetition of phylogeny by ontogeny? If the explanation of the inheritance of acquired characters by means of physiological units were accepted, this law would be futile. For the new physiologic units with changed polarity must take on at once in the daughter organism that form to which the parent organism had last attained, without needing to pass first through the preceding forms.

The physiologic units were devised in order to permit the comparison of the formation of the organism with that of a crystal. But a substance which because of a slight qualitative alteration of its molecules changes its form of crystallization, goes over from the very first commencement of crystallization into a form different from the preceding, and takes on at once the form which it will have after the completion of crystallization. A comparison between organisms and crystals is therefore inadmissible; and this inability is especially evident when it is attempted in this way to explain the laws and phenomena of development, in which organisms and crystals are totally different and are even antagonistic.

Haacke

The conception of Haacke is much like that of Spencer.

"According to my view," says he, "we have to do not only with the genetic continuity of the germ cells of one generation with those of the generation immediately preceding and following, but also with a material continuity

of the germ cells with the other cells of the body. The body represents a system in equilibrium; if this changes the germ cells developing in it change also. But the equilibrium of the system constituted by the body becomes directly altered by the acquisition of new characters; consequently the changes which it undergoes must be transmitted also to the germ cells. But no matter whether the germ cells become changed as a result of the acquisition of new characters by the body which surrounds them, or whether they remain unchanged, they always inherit the same thing, namely, the capacity to form that body with which they were in equilibrium." [174]

Like Spencer he supposes that this equilibrium is due to the tendency possessed by an infinite number of particles, identical throughout the whole organism, to dispose themselves in this way only. His rhomboidal *gemmes,* grouped into composite units or *gemmaria,* are fundamentally nothing else than the physiological units of Spencer. The geometric form attributed to them, which emphasizes the static character of this explanation, does not make it in any way more acceptable.

Nevertheless there are to be noted and carefully considered, here perhaps, even more than in Spencer, the close interaction and the reciprocal equilibrating influence, which would always exist between the soma and the germ substance,—that is to say, between the organism and that small portion of its units contained in the reproductive cells,—not only throughout the whole development of the individual but also after the completion of development when the organism becomes subject to the modifications which external agents induce in it.

[174] Haacke: Kritische Beiträge zur Theorie der Vererbung und Formbildung. Biol. Centralbl., Bd. XV. 1895. P. 568.

Sedgwick

This investigator deduces the possibility of the inheritance of acquired characters from his conception that the pluricellular organism is simply a great syncytium.

"If the protoplasm of the body is essentially a syncytium and the ovum until maturity a part of that syncytium, the separation of the generative products does not differ essentially from the internal gemmation of a protozoan, and the inheritance by the offspring of peculiarities first appearing in the parent, though not explained, is rendered less mysterious; for the protoplasm of the whole body being continuous, we must naturally be inclined to think that every change in the molecular constitution of any parts of it would naturally be expected to spread in time, through the whole mass." [175]

This conception which recalls somewhat Naegeli's idea of an idioplasmic network, extending its meshes throughout the whole body, though it gives a hint of the possible mechanism of inheritance by means of this protoplasmic continuity, nevertheless does not give even the most vague and remote notion of the nature of this mechanism.

Bard

According to this author the cells participate in ontogenetic development in two ways. The first way is by their specific division or qualitative nuclear division, as in Weismann's theory of preformistic germs. The second rests upon a special action of the germ cells upon the somatic cells, acting indeed at a distance but nevertheless

[175]Adam Sedgwick: The Development of the Cape Species of Peripatus. Quart. Journ. of Microscopical Sc. Vol. XXVI. 1886. P. 206.

not by any mediate path, like the influence exerted by electric induction-currents in the production of induced currents, and Bard has therefore given this process the name of *vital induction.*

But this induction would be exercised not merely by the germ cells upon the somatic, but also by the latter upon the former. And the modified soma is capable of bringing about the inheritance of the modifications it has undergone, by means of an influence of exactly this nature exerted upon the germ cells contained in it.[176]

But the inheritance of these new characters by the next succeeding organism by the means of the germ cells which give rise to this latter can be accepted only upon the supposition that it is effected by means of the same vital induction which had already transmitted the characters of the paternal soma into the germ, now acting in the reverse way. And Bard himself seems to admit this. But if this is true for the characters acquired last, it must also be true for all the characters acquired phylogenetically. Consequently the role which specific cell division or qualitative nuclear division in the Weismannian sense would play in the histologic differentiation and in the whole development would become reduced to nothing.

We shall limit ourselves then to drawing attention to the inconceivability, made more evident by the considerations just mentioned, of the idea that the germ cells could participate in the development in two such extremely different modes of action simultaneously, and the lack of any experimental proof for this supposed vital induction.

[176]Bard: Influence spécifique à distance des éléments cellulaires les uns sur les autres. Archives de Médecine expérimentale; 1. série, t. II. Paris, Masson. May 1, 1890; and La spécificité cellulaire et ses principales conséquences. La Semaine Médicale. Paris, March 10, 1894.

Tornier

Tornier believes that the nervous system acts as intermediary, transmitting the acquired characters from the soma to the germ cells and then fixing them in the latter.

"In the more highly organized individuals each adaptation of the active end organs is accompanied by a corresponding and equivalent adaptation in the central nervous system. The central nervous system in its turn transmits the acquired character to the sexual organ forming with it a single functional and nutritive unit, and especially to the sexual cells causing them to undergo an equivalent transformation. When the sexual cells become later generative cells, the property acquired by the parent is by this means inherited by the descendents." [177]

One does not see nevertheless how the modification undergone by the sexual cells could be reversible; that is to say how these cells could produce in the descendants the new character which was acquired by the parent organism and to which their own modification was due. To state it more exactly, one does not see at all how it will have satisfied the condition to which we shall often have occasion to return, and which appears indispensable to this reversibility, namely that during ontogeny there is produced at the right time and the right place an action, which is of exactly the same nature as that by which this part of the paternal soma had reacted to the modifying action of external influences.

It is necessary nevertheless to note the important role which is thus attributed to the nervous system as the in-

[177]Tornier: Über Hyperdaktylie, Regeneration und Vererbung. Arch. f. Entwicklungsmech. d. Org. Bd. III. Heft 4. and Bd. IV. Heft 1. Leipzig, Engelmann. 1896. P. 192.

termediary through which must pass all the characters newly acquired by the soma and thanks to which they become transformed so that they can then be inherited by following generations.

Oscar Hertwig

Oscar Hertwig gives in the following words the essentials of his theory of biogenesis.

"The cells, necessarily equal specifically on account of their origin in the segmentation of the egg, which are combined to constitute an organic system of a higher order, have their character determined by the relations in which they become placed during the course of development. Their state becomes modified when these relations are modified. For the cell organism is an extremely irritable substance so that the slightest influences are sufficient to bring about modifications in it."

"Contrary to the mosaic theory of Roux and the germ plasm theory of Weismann, the theory of biogenesis is based upon the principle, that from the commencement of development, the cells arising from the segmentation of the egg are constantly in the most intimate relation with one another, and the character of the developmental process is determined essentially by this fact. The cells do not take their especial future character of their own initiative, but their character becomes determined according to laws which result from the co-operative action of all the cells during the successive stages of development of the entire organism."

"The relations of the rapidly multiplying cells of the substance capable of development are constantly changing in accordance with general laws, and the relations between these internal factors and those which are with-

out the organism are likewise undergoing continual change, and because of these changes in relations new conformations become produced at each stage of the developmental process in a variety becoming ever more complex." [178]

Nevertheless this does not hinder one, according to that investigator, from considering the organism in its entirety as a single physiological unit because of the idioplasmic identity of the nuclei of all its cells;—a thing which he thinks, makes the inheritance of acquired characters conceivable.[179]

For to explain the latter, Hertwig brings up the cases of infection, immunization, and other similar examples, in relation to which the organism can really be regarded as a single entity. He quotes for instance the experiments of Ehrlich who has succeeded by the administration of extremely small doses of ricin in making rats immune to this poison which is very powerful for them, and in establishing the fact that this immunity was acquired not only by the walls of the digestive canal with which the poison comes into immediate contact, but also by all the other tissues of the body, such as for example the subcutaneous tissues and the ocular conjunctiva, and even by the germ cells as was proved by the fact of the transmission of this immunity to the young born of immunized parents.[180]

Just as all the cells of the body are accessible to the action of ricin and thanks to that fact all undergo a material modification, which some of them, namely the germ cells, transmit later to the descendants as an im-

[178]Oscar Hertwig: Die Zelle und die Gewebe. II. P. 75, 144, 156.
[179]Oscar Hertwig: Ibid. II. P. 241.
[180]Oscar Hertwig: Ibid. II. P. 240ff.

munity against ricin, just so according to Hertwig's view do all the cells behave toward acquired characters in general. "In the same way as the cell is sensitive to the action of ricin, which brings about an enduring material modification of it, and this becomes inherited as immunity to ricin, so I think every cell is sensitive also to the influence of the general condition of the body, which brings about material modifications of its substance, that is of its idioplasm or hereditary material, which is especially susceptible of such material modifications, and these correspond to the cause as its effect both in the cells of the soma and also in the sexual products." [181]

We shall not consider here the fact demonstrated by Ehrlich, that in the instance in which only one of the parents was immunized, the immunity was transmitted very well to the young of an immunized mother but on the contrary was not transmitted to the young of an immunized father; a fact which seems to confirm the hypothesis of Ehrlich that the immunity against ricin was due to the formation of an anti-ricin, with which the protoplasm of all the cells became impregnated, but with which the spermatazoon could not become impregnated because it is almost entirely devoid of protoplasm, showing consequently that one has to do here not at all with a permanent modification of the nuclear idioplasm. But even apart from that and even admitting the hypothesis that the immunity against ricin was due from the beginning or at the time to the acquisition by the idioplasm of a new and persistent character,[182] it is still evident that this is not a just comparison.

For in the case of infections, immunizations, and so

[181]Oscar Hertwig: Ibid. II. P. 242.
[182]Oscar Hertwig: Ibid. P. 241.

on, there would be a single identical influence exerted upon the nuclei of all the cells without exception, which makes it conceivable that thereby the special nuclei of the different cells, and consequently of the germ cells also, could all inherit the new reactive property, which would be added to the other special characters already present in each nucleus and different in the different cells.

But in the case, for instance, of a certain muscle, which develops to a greater size because of a definite modification in its local, trophic, functional stimulus, is it possible to make the analogous statement that there is thus obtained a new state of the body which brings about a modification in the idioplasmic substance of all the cells of the organism without exception—the same modification in each of them? Certainly this modification induced in the trophic functional stimulus of a muscle and the greater development thereby provoked in it will exert an influence on all or nearly all parts of the organism; but the most probable supposition and that best corresponding with the facts would be that the reaction is different in each part. This case at least is quite different from that in which one has to do with the transmission of a definite infection or immunity, and cannot be compared with it without further consideration.

In short Hertwig supposes that every local material modification which appears at a given point of the idioplasm as a reaction to a new functional stimulus extends at once throughout the whole idioplasm, so that the latter becomes modified uniformly everywhere, like a true physiologic unit:

"In the organism considered as a physiologic unit of life the actions of all individual organs, tissues and cells must be combined into a complex common action, the

nature of which will be conditional upon the general state of the organism; this action will be felt by each individual part and in so far as it amounts to a lasting modification of the idioplasm it becomes a newly acquired character."

At every fresh modification of the general state of the organism, "the total heritage of the organism becomes enriched by a new member, by a new anlage which manifests itself again in the development of the succeeding organism, in that now the newly developing individual reproduces more or less 'from the germ out' or from internal causes the character which its parents had acquired during their lives from intercourse with the outer world." [183]

Does Hertwig in this say that the reproductive substance is constituted by a heaping up of a whole series of material modifications, which correspond to the successive phylogenetic general states of the body, and constitute as many potential tendencies?

That is hard to decide, because all that relates to his conception of the idioplasm structure is obscure and often contradictory. Thus in some places he seems to admit that his idioplasm may be constituted by preformistic germs, so that his theory would belong with that of De Vries to the group of theories of epigenesis with preformistic germs. In other places on the contrary where he speaks of general states of the idioplasm, and other similar things, every idea of preformistic germs seems to be excluded, so that his theory appears to be very similar to those of epigenesis without preformistic germs, like that of Spencer. The same is true also of this heaping up of different material modifications representing the suc-

[183]Oscar Hertwig: Ibid. II. P. 242, 243.

cessive phylogenetic states; he appears sometimes to exclude, sometimes to accept it.

If he accepts this heaping up, the explanation of the inheritance of acquired characters which the hypothesis of biogenesis could give would be reduced to this:

The uniform modification into which are summed up during their extension throughout the whole body the different transformations in the idioplasmic nuclear substance that are brought about in consequence of the acquisition of new local characters is added to the preceding phylogenetic modifications without altering them, but merely reducing them to the potential state. Then in the next following ontogeny, when the required stage of development is attained, and this recently acquired idioplasmic modification becomes active in its turn, it induces the same general state of the body as was induced in the parent as a result of the acquisition of new local characters, and this general state, because of the reversibility of the relation between action and reaction, tends to bring about the formation of this character once again.

But one must not be deceived even by this. Even supposing this to be the explanation that the biogenetic hypothesis could afford for the inheritance of acquired characters, it would consist rather in mere words than in ideas. For, as we have said above, this supposed summing up of all these different, simultaneous, local variations into a single idioplasmic modification, including them all and uniform for the entire organism, lacks not only any basis in fact but also any possibility of conception. And the following questions remain unanswered: In what do these different general states of the idioplasm consist? In what way do some come to be added to the others

during ontogeny one after another in the same order as in phylogeny? How does each of the successive general states of the idioplasm, identical for the entire organism, exert upon each individual cell so many special actions, which are not only quite different from one another but also are the exact reverse of those which by their union had produced this general state during phylogeny?

But however that may be, it is not at all certain that Hertwig accepts this heaping up. For, as we have said above, if he seems in certain places inclined to accept it, he appears in others to reject it absolutely.

He seems to accept it for example when he approves and adopts the following passage from Nägeli:

"The unfolding of the anlagen of the idioplasm follows faithfully the phylogenetic order. While the organism, developing in ontogeny, runs successively through the stages through which its phylogenetic stem has run, the idioplasmatic anlagen become developed in just that order in which they came into existence."

And this conception appears confirmed in the following words of Hertwig: "On account of the progressive multiplication of the cells, their combined action is constantly producing new embryonic states in the same serial order as that in which they appeared during phylogeny. The individual cells are brought into new relations to one another and to the external world, and through these successive reciprocal relations the anlagen latent in the cells become awakened." [184]

In other places on the contrary he seems to reject completely this heaping up of a whole series of anlagen, of which each should correspond to the phylogenetic state

[184] Oscar Hertwig: Die Zelle und die Gewebe. II. P. 251, 253.

in which it had arisen, and to suppose instead that when once the idioplasm has been modified there remains in it nothing more of the preceding states, not even in a latent or potential condition. At least this would seem to be indicated in the following passages.

"The theory of biogenesis makes it necessary for us to introduce into Haeckel's statement of the fundamental biogenetic law, a few modifications and explanatory additions through which the contradiction (between this law and this theory) may be avoided. We should drop the expression: repetition of the forms of extinct ancestors, and substitute for it: repetition of forms which obey the laws of organic development and which progress from the simple to the complex. We should lay the emphasis upon this, that in embryonic forms, just as in the adult forms of animals, are expressed general laws of development of organized living substance."

"The periodically repeated development of pluricellular individuals from unicellular representatives of the species, or individual ontogeny, is brought about in general accordance with the same rules as the preceding ontogenies, but becomes each time a little modified corresponding to the extent to which the characteristic cell of the species was modified in phylogeny."

"That certain conditions of form recur in the development of animals with such great constancy, and in the main in similar ways, is due chiefly to the fact that in all circumstances they furnish the prerequisite conditions under which the next later stages of ontogeny can be produced."

"The unicellular organism, on account of its very nature, can be transformed into a pluricellular organism

only by division. It follows that in all living beings ontogeny must commence by the cleavage process."

"An organism constituted by layers and groups of cells disposed in a definite order can be formed from a heap of cells only on condition that the cells while they are multiplying, begin to be arranged in separate assemblages and so progress in accordance with certain rules from the very simple initial forms to more complex ones. Thus the gastrula implies as prerequisite the simpler stage of the germinal vesicle. Thus the embryonic cells must first be disposed in germinal layers, which constitute the basis for further processes of differentiation in their territory. The anlage of an eye in a vertebrate can be formed only after a nerve tube has been separated from the outer germinal layer, since in it is included also the material for the formation of the optic vesicles."

"Certain forms then become firmly fixed in the developmental process, despite all the constantly acting, modifying factors, because it is only by means of them that the complicated final state can be reached in the most simple way and in the most suitable manner." [185]

Thus as we said, Hertwig seems in this really to suppose, contrary to what he asserted above, that the idioplasm is not at all a heaping up of numerous anlagen representing respectively the successive steps of the evolution of the species, but so transforms itself with each new phyletic acquisition that it preserves no trace of preceding phyletic states.

In this he is in complete accord with the hypothesis of Spencer, from which in fact he quotes long passages and makes them his own. And accordingly he supposes,

[185]Oscar Hertwig: Die Zelle und die Gewebe. II. P. 273, 274, 276.

as appears from his own words here quoted, that if the organism appears to pass again during ontogeny through the preceding phyletic stages this depends merely upon the fact that there is no other materially possible way for the idioplasm to attain the phylogenetic equilibrium just acquired.

But to accept this is to deny the law of repetition.

One notes that Hertwig was lead to reject this law, as he himself admits, only because he wished to avoid the objection which Weismann had already urged against Nägeli; namely that if one supposes that different phylogenetic forms may be due to respective idioplasms qualitatively different from one another it is not possible to understand how the same forms when they succeed one another in the ontogeny of a single species can then depend only upon "different conditions of tension and movement," of one and the same idioplasm.

But it seems to us that Hertwig has attempted in vain to circumvent this obstacle.

"A very general and very astonishing fact," writes Delage, "is that ontogeny almost never follows a direct and simple course. The cells almost never dispose themselves from the beginning in the order which would bring the embryo soonest to its final conformation. Ontogeny approaches its goal gradually, but as though compelled to tack against a contrary wind, and its long tacks carry it sometimes far to the side. It shapes a number of rudiments, permits purposeless members to arise, opens gill clefts in a lung breathing animal only to close them again, and so on." [186]

These tacks, these deviations hither and thither, cer-

[186]Delage: L'hérédité etc. P. 175—176.

tainly do not denote any endeavor of the idioplasmic substance to proceed by the shortest route to the condition of its equilibrium. They indicate that it is quite impossible on the one hand to accept the passage of ontogenetic through phylogenetic forms and on the other hand to refuse to this process the significance of an actual repetition of phylogeny by ontogeny. In other words one must seek the cause of this repetition not merely in biologic laws of maintenance of the equilibrium in an existing homogeneous idioplasm, but chiefly in the entire past of the species and just in the historic fact that it passed during its development through such and such phylogenetic forms.

And so the objection urged by Weismann against Nägeli can be urged in its full force and even more justly against Hertwig. For though Nägeli gave no explanation of their causes and ways of action, he nevertheless accepted the activation of a whole series of different anlagen of the idioplasm in exactly the same serial order as in their phylogenetic appearance. Hertwig on the contrary after he had first accepted this activation of successive anlagen of the idioplasm finally rejected it.

Driesch

This author's conception of organic development cannot in its very nature afford any explanation whatever of the inheritance of acquired characters and consequently, admitting that this inheritance exists, ought for this very reason to be considered inadmissible. It can be summed up in the following words of its author.

"Each cell concerned in the ontogenesis in so far as it possesses a nucleus really carries within it the sum total of all anlagen; in so far however as it possesses a specific

protoplasmic body it is, just on account of this latter, susceptible of being acted upon by only certain causes (causes which effect the liberation of different individual nuclear energies)."

"We believe that the capacity of reacting to stimuli resides in the nucleus, but that the capacity of receiving them resides in the protoplasm, which is chemically specific in each elementary organ. The protoplasm is thus the medium, (the zone of perception), between the liberating causes and the nucleus, (the zone of action)."

"The appearance of elementary processes comes about in each ontogeny through a liberation of potentialities. * * * I break the whole of ontogeny up into a series of liberated effects."

"Each liberating cause produces not only a chemical specificity and thereby the new elementary process as such, but it produces through this specificity at the same time the limitation by which the new cell is capable of receiving later only certain further liberating causes." [187]

The especially striking thing in this conception is the absence of any real, continuous, reciprocal dependence of the different parts one upon another throughout the whole course of development. Each cell will preserve in its nucleus, it is true, the germinal substance uninjured; but the successive liberation of special nuclear energies which will impart to it its own especial character, depends fundamentally only upon the specific properties which its protoplasm had already acquired earlier, and not upon the reciprocal actions which exist between all parts of the body throughout the whole duration of ontogeny, as it would according to Hertwig's theory, for instance.

[187]Driesch: Analytische Theorie der organischen Entwicklung. P. 81, 49, 60, 82.

For the specific protoplasm which a certain cell has already acquired at a given moment of ontogeny by receiving only one certain stimulus corresponding to its immediately preceding specificity, would really become the special cause by which among all possible nuclear energies only that one becomes liberated which should become active at that instant. The activation of this new nuclear energy would in its turn modify the specificity of the protoplasm of this cell and of its immediate descendants; and this protoplasm so altered would then become the cause of the reception of a new specific stimulus and of the consequent liberation of the next required nuclear energy; and so on up to the completion of development.

Each cell of any given ontogenetic stage would thus come to carry in itself all that is necessary to determine its own future character and that of its most remote descendants, with the exception of the various stimuli which it is the duty of the protoplasm to select and to receive.

One thing is not quite clear in this. Do these liberating causes of the different nuclear energies, that is these stimuli, among which each protoplasm should select and receive only those belonging to it, come only from the world outside the organism, or also from the reciprocal actions of the individual parts in the interior of the organism? In the first case it would be necessary to place Driesch among the out and out evolutionists; in the second, his theory would be a mixed one, that is it would rest upon phenomena of evolutionistic nature combined with others of epigenetic nature.

We shall not set forth any further here what enormous difficulties one would encounter in either case if one sought to build up in accordance with this theory any

conception of a mechanism for the inheritance of acquired characters. Even if the hereditary substance should be preserved in its entirety, and unaltered, in the nuclei of all cells without exception throughout development, this would be ascribable only to qualitatively equal nuclear division. But one could not but ask why the modifications which supervene in the hereditary nuclear substance of such and such somatic cells in consequence of a new local functional adaptation in the adult stage should not remain limited to these cells alone.

Very noteworthy, however, in Driesch's theory is the conception that ontogeny takes place by means of a series of successive liberations of different energies remaining up till then in the potential state, and also that one result of the liberation of each of these energies and of the effects which it produces is that the necessary and sufficient conditions for the liberation of the next following potential energy are brought about.

Herbst

The epigenetic conception of Herbst is still less capable if possible, than that of Driesch of rendering conceivable any mechanism whatever for the inheritance of acquired characters.

He mentions at first several experiments upon the way in which unicellular organisms and cells react to certain stimuli, and also a great number of facts serving to show the great dependence of plant ontogenies especially upon external influences. While it is evident that external influences constitute most often only liberating or releasing stimuli, they seem on the contrary to become in certain formations real formative stimuli. In these formations there is involved not only a true ontogenesis

but an actual phylogenesis which would repeat itself in each generation *ex novo*, because of the repetition always in the same way of the same external formative influence.

After having thus stored up a rich harvest of facts upon the physiological actions exerted by the most different stimuli upon organisms or upon given parts of organisms,—actions which are properly nothing else than functional adaptations in a broad sense of the word,—Herbst believed he was able to build upon them his epigenetic conception, by which he makes development fundamentaly dependent upon a whole series of directive stimuli.

"Just as freely moving organisms are influenced in the direction of their movements by external agents, so do independent tissue cells react to definite directive stimuli, and thereby make possible the production of a large number of ontogenetic formative processes."

"Just as the germinal vesicles of Cuscuta, for example, develop their stinging barbs at the points of contact with the plant upon which they lodge, just as in the leaf stalks of Helleborus niger the traction of a weight causes the formation of new mechanical elements which otherwise do not appear, or just as roots may be made to grow on a grass stalk because of the secretion of a gall fly, so, in the interior of an animal embryo in process of development a given organ can cause new formative processes to come into existence in another organ by means of contact, pressure, traction, by a specific product of metabolism or in some other way."

And so, "just as in plants and sessile animals morphological formations of the most different kinds are produced through formative stimuli which either arise from the external world or are exerted by one organ of

the organism upon another; so also the morphological changes in animal ontogeny arise in the same way through manifold inductive stimuli "Inductionsreize" which are almost always of internal origin." [188]

This conception, especially if it is extended to the whole process of development in general, would really amount to a reduction of ontogeny, exactly as in the plant formations above mentioned in which external agents act as true formative stimuli, almost to a phylogeny, constantly repeating itself anew in each generation. And the fact that successively arising generations would in spite of that remain always alike is to be attributed to the repetition, proceeding always in the same way, of successive functional stimuli both without and within the organism in process of development, which are produced gradually one out of the other through the principle of fructifying causality and give rise each time to these new phylogeneses.

In this respect the conception of Herbst recalls the purely mechanical explanation of development given by His, who refers the appearance of the same ontogenetic phenomena every time to the repetition of definite mechanical influences, proceeding always in the same way. Since each influence, itself induced by the influences preceding it, induces in its turn the influences following it, then if only the first link of the chain is constantly repeated in the same way in each generation, that would be enough to cause the same thing to happen in the case of all the others.

[188]Herbst: Über die Bedeutung der Reizphysiologie für die kausale Auffassung von Vorgängen in der tierischen Ontogenese. Biol. Centralbl. 1894. Bd. XIV. No. 18—22. P. 771; and Bd. XV, N. 20—24. P. 852.

One notes that these theories of Herbst and His and other similar ones imply an extraordinary independence and autonomy even during ontogeny not only in each part of the organism but even in each cell. The development of each particle, even the most minute, would thus depend fundamentally upon the independence of its response to the action of its immediate or close environment, even though this response is given in a very definite manner and is in no wise arbitrary. But this is hard to reconcile with the mutual adaptedness which there must necessarily be between the different parts constituting a single co-ordinated whole. And it is still more irreconcilable with the constancy and precision with which even the most minute peculiarities of the organism are reproduced in each development, even when the conditions of the environment in which it takes place do not always remain alike in respect to nutrition, temperature or other factors.

And so much the more, since the principle of fructifying causality, employed to explain this constancy and rigorous precision with which the same series of ontogenetic phenomena is always repeated, is a sword with two edges. For, admitting that only a single one of the numberless intermediate links of the chain should find itself in a somewhat different condition in relation to its environment, or should differ in any way even though inconsiderably from the corresponding link of the preceding generation, a thing which one might well assert occurs in every ontogeny, then the remaining portions of the chain would find themselves, because of the modifications accumulating and multiplying like an avalanche, altered throughout, and therefore in the last links also. The mutual adaptedness of numberless different parts and their co-ordination into a single harmonious whole, and

the constant precision in the repetition even of the most minute peculiarities, stipulate fundamentally an individual ontogenetic factor, which is directive and at the same time co-ordinative, acting at each moment of development throughout the entire organism even to the smallest single parts of it. But ontogenetic theories like those of Herbst or His take a stand diametrically opposed to this.

It is also almost superfluous to remark that they cannot give the least account of the repetition of phylogeny by ontogeny, and still less of the inheritance of acquired characters.

For the latter, as we can well assert without needing to fear that we get too far from the truth, requires absolutely the condition, certainly not sufficient, yet at least necessary, that just this ontogenetic factor of individual nature should act everywhere and incessantly and also that it should not give up the control of development even for a moment, so that it may thus be in a position to experience in itself each variation even the smallest appearing in the organism in consequence of any new functional adaptation. But the theories of Herbst and His, and all others like them, which have recourse only to the principle of fructifying causality, rest upon the conception that the successive influences would always be left to themselves by their respective special causes, as soon as they had once been produced and launched, so to speak, into development, to produce in their turn new influences.

Therefore these theories necessarily exclude any inheritance of acquired characters. But if this latter actually exists they become, as we have said, quite untenable from this point of view also.

Orr

Orr takes as his starting point the conception that he has formed concerning the way in which the pluricellular organisms arise from the unicellular.

It is easy to understand that after the unicellular organism in the course of generations had attained a certain size, its external surface might have become transformed in consequence of contact stimuli into a denser protective layer, and thereby have lost its reproductive capacity, which would have been preserved only in the inner part of the organism.

"When such an organism as this would be divided into a number of pieces by the natural process of reproduction those parts of the protoplasm which had not undergone a grosser material differentiation would be like the protoplasmic germs of all its ancestors, capable of responding to the same stimuli, and therefore of developing in the same manner. The only difference between these and the ancestral germs would be the increased complexity of their nervous co-ordinations. But, on the other hand, part of the organism which has been differentiated into the denser outer layer would be in structure so different from the germs of the species that it would be incapable of responding to any of their accustomed stimuli and therefore incapable of repeating the development."

"But at every step in the evolution a part of the protoplasm retains its original qualities, only changing its nervous condition to a condition of greater complexity of co-ordinations. In this way the original protoplasm gradually adds to itself the co-ordinations for developing

in each generation, first cell walls, and then the differentiated organs." [189]

From the whole work of Orr it seems to result without any possible doubt, that according to his view this non-differentiated part of the protoplasm is present in all the cells of the organism, is everywhere quite similar, and is continuous to the extent that stimulating influences can be transmitted from any given part whatever to all parts of the animal, so that it constitutes a complete physiological unit.[190]

But on the other hand it is never to be seen quite clearly what this investigator understands by this greater complexity of co-ordination. The fact that the nervous system presides over all physiologic activities of the organism makes him think rightly that development also may be dependent on similar nervous phenomena. Only in the nervous system of the organism is clearly to be seen what is to be understood by a greater complexity of nervous co-ordinations, because it is constituted by numberless points, distinct from one another and connected with one another in more or less complicated ways by direct or indirect nerve tracts. In undifferentiated protoplasm on the contrary, which remains always entirely similar in the most different parts of the body, and *a fortiori* in that infinitely small part contained in the germ cells, one could not conceive in what these supposed nervous co-ordinations and this ever greater complexity of co-ordinations could consist, and what their significance would be.

The following passages do not clear up any of the

[189]Orr: A Theory of Development and Heredity. New York, Macmillan, 1893. P. 127—128.

[190]E. g. Ibid. P. 124.

obscurity: "When we consider the protoplasm's responsiveness to stimuli and to the effects of repetition or practice, with the intricate co-ordinations that may thereby be effected, also the impressions made by stimuli which remain long fixed as "memory," we are led directly to suppose that the property which is the basis of bodily development in organisms is the same property which we recognize as the basis of psychic activity and psychic development."

"On the same principle that a thought in the mind calls up an associated thought, or one tone of music calls up another, or one action in an oft repeated series of actions calls up the next subsequent action or actions, so the initial stimulus being given to an incipient organism, its responsive activity each time tends to produce by association the next activity in the oft repeated series and so on through the successive steps of growth and development." [191]

The points of contact between the mnemonic phenomenon of the association or succession of ideas and the phenomenon of ontogenetic development have already been very rightly brought forward by others and we shall return to them for closer examination in the last chapter. It may be remarked here merely that the first can in no way serve to explain the second. For in the first place it belongs to a class of phenomena still more specialized and more complex than the phenomenon to be explained, in the second place the conditions of origin and of repetition are quite different in the two phenomena.

When a melody strikes the ear for the first time and is later often repeated it leaves behind impressions on

[191]Orr: Ibid. P. 238—239, 142.

several nerve centers and unites them by new nerve tracts becoming always smoother. These new impressions and tracts remain then unaltered in the same places in which they were produced and it is just in their continuance in the place of their origin that there must be sought the reason of the always greater ease with which these melodies are reawakened in our memory. When the muscles of the hand become accustomed to producing a musical exercise, the greater development of the muscles and the greater complexity of the nervous co-ordinations which connect them with the brain constitute well defined material alterations which remain unaltered in the places where they arise and make the exercise, at first difficult, always easier.

In the development of the organism on the contrary the causes of the repetition each time of always the same ontogenetic stages must reside in a single cell, the germ cell. But this cell is not in any way the place in which are produced the material alterations which were acquired by the parent organism and handed over to the descendants, like the stronger development of certain muscles, the greater complexity of certain nervous co-ordinations and other similar variations. Of the stronger development of muscles, of the greater complexity of the nervous co-ordinations which are produced in the parent organism, there remains absolutely nothing, in so far as they represent alterations of muscles and nerves, in the little particle of matter which is destined to produce the descendants.

Consequently the comparison of the two phenomena, although certainly very suggestive, is not sufficient by itself to afford in any way an explanation of ontogenetic phenomena.

Orr continues in these words: "The co-ordination of forces which determines development is not to be considered a definite, localized mechanism, wound up, and ready to go when touched. If such were the case we ought to find one such mechanism allotted to a certain definite number of cells; but instead we find that each piece (of a hydra), regardless of the number of cells, or whether it be the half or the twentieth of the hydra, is capable of producing only one new individual."

"The quality upon which development depends seems to reside in a small piece just as well as in a large piece and moreover equally in all parts."

"I think we can best compare the inheritance of the plan and potentiality of development in the clump of protoplasm to inherence of ideas and potentialities of volition in the brain substance, not as though each idea and potentiality were located there in its own minute definite limited space, and attached to a definite mechanism of matter; but rather we should think of development and mental potentialities as dependent upon certain states of living matter, which states are the result of the entire past history of that living matter and which thus determine the method of response to external stimuli, and the direction which shall be taken by the new energy constantly entering from the outside." [192]

This recalls again the above mentioned conception of Nägeli and Hertwig of idioplasm which is both general and mnemonic, with all its short-comings which consist in complete indefiniteness or worse yet in lack of content masked by empty words.

Nevertheless it is worthy of notice that however

[192]Orr: Ibid. P. 172—173.

indefinite the theory of Orr may be, it contains a clearly expressed and very remarkable idea, namely: the conception that nervous activity is the only general phenomenon and basis of life. Orr attributes to it therefore the great function of forming by itself the whole mechanism of development as well as of the inheritance of acquired characters, and seeks to explain through it the striking analogy between this mechanism and the mnemonic phenomenon.

Cope

In order to explain the inheritance of acquired characters Cope starts out with the following investigations upon butterflies. By exposing larvæ which were near the stage of pupation to different colors, the corresponding colors were produced in the chrysalids developed. In another experiment larvæ, which were in the act of weaving cocoons, on exposure to certain colors were induced to weave cocoons of corresponding colors.

"In the first experiment," explains Cope, "the dynamic effect produced by the exposure was stored for the period which elapsed between the exposure of the larva and the full development of the pupa. The second experiment demonstrates that a stimulus may be transmitted to a gland so as to modify the character of its secretion in a new direction. From both experiments we learn the transmissibility of energy from the point of stimulus to a remote region of the body, and its conversion into growth energy (in this case by physiogenesis). This prepares us to look upon heredity as an allied phenomenon, i. e. the transmission of a special energy from a point of stimulus to the germ cells, and its compo-

sition there with the emphytogenic (inherited) energy into bathmism (or evolutionary energy)." [193]

From this he at once draws the conclusion that as soon as a new character is acquired by the soma in consequence of a definite stimulus, it appears at the same time in the germ plasm also. This simultaneous double acquisition of the same character by the soma and by the germ represents his theory of "diplogenesis:" "The effects of use and disuse are twofold; viz.: the effect on the soma and the effect on the germ plasm. Those who sustain the view that acquired characters are inherited must I believe understand it as thus stated. The character must be potentially acquired by the germ plasm as well as actually by the soma. Those who insist that acquired characters are not inherited forget that the character acquired by the soma is identical with that acquired by the germ plasm, so that the character acquired by the former is inherited but not directly. It is acquired contemporaneously by the germ plasm and inherited from it. There is then truth in the two apparently opposed positions, and they appear to me to be harmonized by this theory of diplogenesis." [194]

It is almost unnecessary in this connection to remark that, if one sticks to the letter, this supposed double acquisition of the same character by the soma and by the germ, lacks any foundation in fact and indeed appears inconceivable. For in the first place the two experiments quoted above concern phenomena too special, too complex, and as yet too little analysed to permit of their utilization as foundations for any theory. In the

[193]Cope: The primary Factors of organic Evolution. Chicago. The Open Court publishing Company. 1896. P. 440.

[194]Cope: Ibid. P. 442, 443.

second place if this character instead of consisting in a general change existing in all the cells concerned, is rather any given local morphological or physiological modification whatever of definite organs or tissues, it will evidently be impossible to represent this modification as acquired at the same time also by the germ plasm, since in the latter these organs and tissues do not exist.

It seems nevertheless that Cope's meaning is that each even local morphological or physiological modification of the soma must always correspond at the same time to a certain specific, dynamic state of the protoplasm in general, and that it is this new dynamic state which would be acquired at the same time by the protoplasm of the soma and by that of the germ.

For to explain "the way in which the influences which acted upon the general structure reach the germ cells," he builds up his "dynamic theory," taken from the domain of molecular physics, and has recourse to that special form of energy mentioned above, which he calls "bathmism." And this bathmism would consist acording to this author "in a mode of motion of the molecules of living protoplasm by which the latter build tissue at particular points, and do not do so at other points."

"This action is most easily observed in the beginnings of growth, as in the segmentation of the oosperm, the formation of the blastodermic layers, of the gastrula, of the primitive groove, etc. In the meroblastic embryo the energy is evidently in excess at one point of the oosperm and in defect at another. This is a simple example of the location of growth force or bathmism. In all folding or invagination there is excess of growth at the region which becomes the convex space of the fold; i. e. a location or especial activity of bathmism at

that point. All modifications of form can thus be traced to activity of this energy at particular points."

"The building energy being thus understood to be a mode of molecular motion, we are not at liberty to suppose that its existence is dependent on the dimensions of the organic body which exhibits it. It is as characteristic of the organic unit or plastidule as the mode of motion which builds the crystal is of the simplest molecular aggregate from which the crystal arises. Bathmism has, however, no other resemblance to crystalloid cohesion. The latter is a simple energy which acts within geometrically related spaces, without regard to anything else than the present compulsion of superior weight-energy. In bathmism we see the resultant of innumerable antecedent influences, which builds an organism constructed for adaptation to the varied and irregularly occuring contingencies which characterize the life of living beings. As this resultant is distinctive for every species, bathmism must be regarded as a generic term, and the characteristic growth energy of each species as distinct species of energy, which present also diversities expressive of the peculiarities of individuals." [195]

It would be superfluous to bring forward the extraordinary indefiniteness and, we can almost say, pure verbalism without any foundation in fact of this theory of Cope's which approximates closely Haeckel's theory of perigenesis with its undulatory plastidular movement. We shall confine ourselves to remarking merely that each given dynamic state of the protoplasm peculiar to a given species, when it thus represents in itself the resultant of all dynamic states, which were peculiar to the

[195]Cope: Ibid. P. 447—449.

protoplasm during the whole course of phylogeny, would nevertheless not cease on that account to constitute still a special dynamic state which is quite different from the preceding ones, and which cannot possibly preserve materially even the smallest trace of them. Therefore this theory of Cope leaves the repetition of phylogeny by ontogeny quite as incomprehensible as did that of Haeckel. And on the other hand one cannot see how the protoplasm could be in the same identical dynamic state in all the most different parts of the soma and yet give rise to specific biologic phenomena correspondingly different in each of these parts.

It would have been on the contrary a much more suggestive idea, had Cope sought to reduce all the different, contemporaneous, physiological and morphological variations of the organism, not so much to a single and everywhere uniform change of this given growth energy, as rather to numerous specific variations of a single generic form of energy, so that the latter would thus represent to a certain extent the common denominator of all these unlike morphological and physiological variations. For this is in any case one of the means which every theory must employ which essays to explain the inheritance of acquired characters. For when once all variations of the most manifold forms of energy, acting simultaneously upon the most different points of the organism, are attributed to as many specific variations of a single form of energy as the basis common to all of them, then it would be easy to combine with it the conception that for each complex state of the organism there might appear in the germ a single, well defined specific mode of being of this common form of energy, as the resultant of all these specific different modes

which are active simultaneously, each in its own way in the most different points of the soma. And just as the resultant of several forces acting upon one point at the same moment can be decomposed again into its former component parts, all of which would still act simultaneously, so it is conceivable how this particular mode of being of the common form of energy which arose and was stored up in this way in the germ can become decomposed again at the proper time at all the various points of the new organism into the same modes of being as formerly, which had already been its components in the parent organism.

To mitigate the fault of indefiniteness in his theory this investigator, just like Haeckel, Orr and many others, also compares the ontogeny thus produced by bathmism with the mnemonic phenomenon. And although he has thereby certainly neither removed or even diminished the general vagueness which characterizes his whole theory he succeeds nevertheless in expressing here a remarkable and suggestive idea.

"We may compare the building of the embryo to the unfolding of a record or memory which is stored in the central nervous system of the parent and impressed in greater or less part on the germ plasm during its construction, in the order in which it was stored. This record may be supposed to be woven into the texture of every organic cell and to be destroyed by specialization in modified cells in proportion as they are incapable of reproducing anything but themselves."

"In the case of the germ plasma no other specialization exists so that the entire record may be repeated stage after stage, thus producing the succession of type-structures which embryology has made familiar to us.

In the process of embryonic growth, one mode of motion would generate its sucessor in obedience to the molecular structural record first laid down in the ovum and spermatozooid, and then combined and recomposed on the union of the two in the oöspore, or fertilized ovum."

"Were all cells identical in characters, every one would retain the structural record or memory of its past physical history as do the unicellular organisms. Evolution has however so modified most of the structural units of the organic body that none but the nervous and reproductive cells retain this record in greater or less perfection. The nervous cells have been specialized as the recipients of new impressions, and the excitors of definite corresponding movements in the cells of the remainder of the organism. The somatic cells retain only the record or memory of their special function. On the other hand the reproductive cells which most nearly resemble the independent unicellular organisms, retain first the impression received during their primitive unicellular ancestral condition; and second, those which they have acquired through the organism of which they have been and are only a part." [196]

As we shall devote ourselves in the last chapter to the comparison of the ontogenetic phenomenon with the mnemonic, it will suffice here to bring forward, as a contradiction to the same author's assertion reported above in respect to a single dynamic mode in the whole organism, the complete mnemonic somatization of the specialized somatic cells, or nuclear somatization, which this investigator recognized, and also his suggestive substantial equalization of the nerve cells with the repro-

[196]Cope: Ibid. P. 451—453.

ductive cells as the only cells endowed with unsomatized memory, and consequently as the only ones which would be likewise capable of preserving more or less completely the memory of past generations. Nevertheless he should in our opinion have limited this equalization with the reproductive cells to those nerve cells which are least differentiated.

Delage

According to Delage, "The egg is like a star thrown out by an initial force into the midst of a system of stars in movement. Its trajectory will be influenced and determined by all the stars whose sphere of action it traverses, but nevertheless, if anything had been altered in its mass or in its initial movement, it would not have been what it is. It is not dependent on the system alone nor is it at any point independent of it. Every other similar mass thrown out at the same point, with the same force in the same direction will reproduce a trajectory identical with its own; but every difference even the most minute, in any one of these three factors will be able to induce considerable differences in the form of this curve." [197]

This comparison leaves the repetition of phylogeny by ontogeny and the inheritance of acquired characters out of consideration.

The inheritance of acquired characters is nevertheless accepted in part at least by Delage, who explains it thus: "When a new chemical compound introduced into the organism produces different effects at different points, that is undoubtedly due to this, that it finds at each

[197]Delage: L'hérédité etc. P. 802—803.

individual point a different cell substance as the predominant element. Then if the egg contains the substance characteristic of certain cells of the organism, it must be affected at the same time as these cells and by the same influences. According as these influences exert an exciting or depressing influence and so provoke the corresponding organ to further development or to atrophy, there will be produced a similar action in the egg, the corresponding substances will undergo a certain growth or a certain regression and when the egg develops, the cells whose task it is to localize these substances within them, will experience the effects of this regression or of this growth." [198]

In the first place it is to be noted here that the organs whose modifications produce new phyletic stages do not usually either develop or atrophy uniformly in all directions. Indeed, specific morphological alteration consists rather in a growth or diminution always proportionally unlike in different directions. The particular substance which has increased in the egg can serve at most for the explanation of a quantitative increase in mass of the organ, but not for a morphological increase, different in each different direction, like that which the parent organism has experienced.

In the second place this explanation cannot be satisfactory since there may be growth in one organ, while another organ consisting of the same tissue, such as nervous, muscular, bony tissue, etc., may remain unchanged or even regress. These organs consisting of the same tissue ought all to grow or diminish alike with

[198]Delage: Ibid. P. 837.

each change which their particular substance experiences in the egg.

In the third place, this would at all events suffice only for the explanation of inheritance of those characters which develop in the parent organism under the influence of definite chemical actions, distributed throughout the whole body, and acting only upon those particles or cells of the body which have a certain chemical composition. But what explanation could that give of true morphological inheritance and so of the inheritability of the growth or of the atrophy of an organ resulting from too much or too little use?—of the inheritability of the spongy structure of bone, of the conformation of the eye, and of all functional adaptations in general?

Yet Delage gives the following explanation of the inheritance of the atrophy of unused organs.

"That only is determined in the egg, which is not determined by functional excitation, but the amount determined by the latter is enormous." The absolute uselessness of slight reductions of the atrophied femur of the whale and the consequent inefficacy, in this respect, of natural selection, and on the other hand, the impossibility of understanding how the slight reduction in volume which the femur undergoes during the life of the individual can extend its influence to the egg, and determine in that the modification necessary for the reproduction, in the following generations, of this new reduction in volume, "forces us to admit," continues the author, "that neither in consequence of a fortuitous variation fixed by natural selection, nor in consequence of an acquired and inherited modification does the egg of the existing whale differ in so far as the femur is concerned, from the eggs which produced the whales

of centuries ago, whose femur was only a very little greater than that of the whales of today."

It still remains then to explain, without devising some improbable hypothesis, how the same kind of egg can produce two different forms. And that is not very difficult when one keeps functional excitation in mind."

"When an animal has a femur 20 cm. long, that does not indicate that in its egg all the conditions were present for the formation of a bone of this length. That indicates only that the elements necessary for it are there, which with the co-operation of the functional stimulus can form a femur of such length. We cannot know just what part this latter takes in the result, but it must be considerable."

"While the whale had still a femur, which though not normal was yet only half atrophied, the femur producing factors inherent in the egg were perhaps sufficient to produce a bone of only the size of that present in the whales of today, and the functional stimulus, which as Roux has shown, begins to operate even in embryonal life, did the rest. It is therefore not astonishing that upon the cessation of the functional stimulus, the femur became reduced to a very little rudiment." [199]

But the embryonal functional stimulus in the whales of many centuries ago whose femurs were only a very little bigger than those of the whales of today, cannot have been different from the embryonal functional stimulus of the whales of today, no matter how much one may limit direct morphological action of the egg, if one starts out from the hypothesis that the eggs concerned are quite identical. Why should the embryonal functional stimu-

[199]Delage: Ibid. P. 854—857.

lus in respect to the useless femur, already so atrophied, have been greater in the former than in the latter? The progressive diminution of the femur remains thus entirely unexplained.

Finally Delage accounts for the parallelism between ontogeny and phylogeny in the following way:

"The functional stimulus appears, we agree with Roux, even in embryonal life, but is at this time certainly weaker than after birth. There results from that a noteworthy consequence which escaped Roux. That is that at least the relative atrophy of the organ becomes more marked the older the animal becomes, and that, in respect to the atrophied organ, the young, and above all the embryo, must differ much less from the ancestral forms. Thus there is explained at once the parallelism between ontogeny and phylogeny in everything which is dependent upon atrophy or hypertrophy induced by use or disuse, that is in very many cases." [200]

Is it inactivity that really causes in serpents the retrogression during embryonal life of the already partially developed limbs? Or is it use that in the salamanders causes to any extent the development, during embryonal life, of the same limbs? Whence come these very unlike embryonal processes of activity or inactivity? Why did not this same inactivity, consequently this same atrophy, show itself in the embryos of the remote ancestors of the serpents of today? Why does the inactivity and consequently the atrophy of these extremities depend, in the egg of the present day serpents, upon conditions within the embryonic organism itself, and manifest itself at exactly that ontogenetic moment, which corresponds

[200]Delage: Ibid. P. 856—857.

to the phylogenetic moment at which it was produced in their ancestors, whereas in the latter this reaction commenced only when the animal was exposed, after leaving the egg, to the influences of the external world, and was rendered necessary only in consequence of very definite circumstances external to the organism? We see thus that the question of the repetition of phylogeny by ontogeny finds no answer at all. It seems to us further that there remains only the erroneous view that entire phylogenetic epochs could have gone by, without leaving behind any trace in the egg, so that the progress of each ontogeny would be nothing else than a phylogeny which is almost entirely repeated each time.

In the second edition of his work Delage recognized himself that the significance attributed by him to the functional stimulus in ontogeny is exaggerated.[201] And he admits that he was embarrassed in explaining by it both the special fact of the formation of an organ so complicated and so well adapted to its purpose as the eye, for which during embryonal life there was nevertheless lacking any functional stimulus, and also the phenomena of regeneration, or the general fact that nearly all organs without exception show, from the first stages of their development on, an adaptation to the functions which they will perform only later.[202]

LeDantec

According to LeDantec's theory, each individual, living, elementary mass or plastid "contains a mixture of different plastic substances, which are distributed in such a way that assimilation represented by the equation:

[201]Delage: Ibid. P. 862. Remark.
[202]Delage: Ibid. P. 870.

$a + Q = \lambda\ a + R$ (where a = mass of each single specific assimilating substance; Q = mass of the nutritive substances absorbed; λ = coefficient > 1; and R = mass of the substances of refuse), multiplies all these substances and preserves to them their original proportions. Destruction however, or at least certain destructions, act separately on each of these substances and alter the proportions of the mixture and consequently the characters of the plastid." [203]

From this it appears that LeDantec attributes all variations which the plastids or organisms in general can undergo, to total or partial destructions of the different, particular plastic substances (a) already present, but never to the production of new plastic substances. The numbers and characters of plastic substances, which participate in the formation of the complex substance of the plastid or rather of the organism in general, may be different in different species. The difference between different species and between different individuals of the same species, would consist only in the proportions in which the special plastic substances (a) peculiar to this species, are united.

"We are inclined to regard the living substances of the plastids as mixtures of different plastic substances, the substances (a). The species of the plastids would be determined by the nature or quality of these plastic substances; their individual peculiarities, their personality, would depend upon the proportions of the mixture of these specific plastic substances. In the same way we must regard the individual substances in the higher organisms as characterized by a mixture in definite proportions of

[203] Le Dantec: Traité de Biologie. P. 93.

the living substances characteristic of their species. We are able in this way to present even a mathematical definition of the personality of a given individual of a species, to a certain extent an arithmetical personal description of this individual, namely the list of co-efficients of the mixture of his specific substances." [204]

The proportions of this mixture persist unaltered in all cells of the same organism. Upon this mixture depends the quality of the chemical reactions, i. e. of the molecular movements; upon these latter again depend the molar movements or osmotic currents of nutritive and excretive material; upon the molar movement finally depends the form of each plastid as well as that of the most complicated organism:

"It is absolutely useless to suppose, in the egg which produces man, other characters present than for example those of a simple hepatic or epithelial assimilative element, determining by this assimilation the molar movements around it. These molar movements associated with the movements which result from assimilation in neighboring elements, and also with the existence of the skeleton such as is constituted in a thenceforth unchangeable form from the moment of its first anlage, determine the conditions of local equilibrium from which the local form of the body results. Analogously as soon as a human element (the fecundated egg) is capable of living by itself alone, the molar movements, which assimilation provokes first in this element alone and later in all which are derived from it, determine the successive forms of the growing mass arising from assimilation. The phenomenon appears from the outside then to be

[204] Le Dantec: Ibid. P. 267.

quite otherwise than as though this element had assimilated without being isolated, as though for example it had belonged to a man in process of growth. It would then have been the destiny of this element, thanks to the combined "dynamisms" of the neighboring elements, to build up a part of the man, but not a whole man." [205]

Finally the transformations to which the living substance would be forced by the constraint of external influences may be hereditary, i. e. can take place anew in the descendant organism without any further need of the action of the same constraint, because they would alter the living substance itself in a corresponding way, so that it adapts itself to the new conditions of equilibrium:

"If assimilation were the only possible phenomenon of living matter there would not take place any alteration of the living substance through external influences; but upon the truly vital phenomena of assimilation are superimposed as we have seen phenomena of destruction, and the co-operation of these two phenomena can result in changes in the nature of the substance, in the definite proportions of the mixture forming it; thus education can modify heredity."

"Since the form is the result of the molar movements of the metabolism of all cells of the body, a variation imposed on the form reacts upon these molar movements by which again the molecular movements in the interior of the cell are determined. Then in consequence of this form imposed on the body mass, there will occur within the cells phenomena of destruction, i. e., of variation. The variations may take any direction

[205] Le Dantec: Ibid. P. 257—258.

whatever; but natural selection (which acts in each cell of the organism among the different plastidular variations) intervenes and fixes only those which are adapted to the new conditions of equilibrium." [206]

We would just remark here, that the alteration undergone by the molar movements within each cell will be different in the different cells. For it would be incomprehensible how in the very complex structure of the organism, a local change of form, imposed by external agents, could induce quite identical alterations in the molar movements of all the other cells of the body indiscriminately. Consequently the alterations of the living substance which internal natural selection preserves as fittest will likewise be different in different cells. How then can there be any question of the survival, in consequence of this internal natural selection, of one single plastidular variation identical at all points of the organism?

LeDantec, like Hertwig, has recourse to the example of immunization. But as we have already seen, this case is quite different from the more or less local changes of form, which individuals experience in consequence of particular functional adaptations. In the case of immunization the transforming cause, i. e. antibacterion, is the same for all cells. In the case of a morphological alteration on the contrary the transforming cause, that is, as we would concede it, the variation experienced by the molar movement concerned, is different in each cell.

Even if one were willing to assume an identical variation of the living substance at all points of the organism indiscriminately, that would not explain the

[206] Le Dantec: Ibid. P. 270, 298.

law of the repetition of phylogeny by ontogeny, as we have already had occasion to remark in connection with the similar hypotheses of Spencer, Hertwig and several others. This requires, as we have seen, the conception of the addition of a new substance to all those formerly present.

All variations of the organism are ascribed by LeDantec, as we have already seen, to total or partial destruction of some of the different plastic substances (a), which make up the living substance, whereby their quantitative proportions become changed; but never to the formation of new plastic substances. Likewise different species would differ from one another in the number and quality of the plastic substances (a). From this it follows: 1, that no further development can be effected by any given living matter, if the number of its substances has become very small, and thus an absolute inalterability must be established as soon as this number is reduced to one; 2, that the development of the species can have been produced only by successive total destructions of an always greater number of these plastic substances; 3, that the further a species is developed, the smaller therefore must be the number of the plastic substances which form its respective living matter. One would thus arrive at the absurdity, that the simpler the living substance is the more complex must be the organisms formed from it.

Finally LeDantec, like Spencer, Hertwig and the others is unable to explain histological differentiation by this supposed similarity of living substance in all parts of the organism:

"A muscular element differs entirely from a nervous epithelial element, and these differences are manifested

not only in the form of cells but also in their mode of activity. Now what is the nature of these differences? We do not know. Are they physical in character? That would be hard to believe, because of the difference of the chemical excreta of these elements. If the differences are of chemical nature they must leave uninjured the hereditary patrimony (the living substance similar at all points of the organism). Now it is entirely impossible that quantitative variations can be produced in the elements, and leave untouched a quantitative character already present. Perhaps there is properly speaking no quantitative variation, but only a modification in the nature of the non-living accessory substances which fill out the aggregate at different points of the organism according to the special conditions obtaining at these points. To all these questions we have as yet no answer." [207]

Before we leave this investigator we must bring up one last point, namely: the logical necessity which forces him to regard the living substance as similar at all points of the organism. According to him, this conception is a logical consequence of the inheritance of acquired characters which he holds as a fact already proved beyond a doubt. For, says he, let us consider any given morphological variation acquired by the organism and transmissible to its descendant. And let us assume that the hereditary patrimony, i. e. the living substance (α), originally common to all elements of the individual by descent from the egg, can, under the influence of the morphological variation experienced by the latter, have been replaced, here by a different substance (β), there

[207] Le Dantec: Ibid. P. 461—462.

by another substance (γ) and so on, in such a way that the whole of the "dynamism" existing in this heterogeneous mass, finds its expression in a form of equilibrium F, which preserves accurately, without any need of further constraint, those forms of equilibrium which the individual had acquired in consequence of the compulsion of external influences.

"If that were so," continues LeDantec, "this form could not be hereditary. For the substance β produces the form F only with the assistance of cells of the substances γ and δ , which are simultaneously present in other elements of the altered individual, and no one of these substances which does not belong to the sum total of the elements is by itself a consequence of the total form F. If then one detaches from this form a few pieces capable of reproducing themselves, these pieces endowed with different substances or heritages will give rise to different individuals, namely to individuals or groups of cells like those whose total constituted the form F, but of which none had this form. There is thus absolutely no reason existing why any one of these individuals should take the form F. If then observation teaches us that acquired characters can be inherited we are thus obliged to suppose that in the case in which they are hereditary they were acquired by the parent organism in a homogeneous manner." [208]

Thus if it were possible to explain this inheritance and at the same time to accept, nevertheless, the most complete diversity of the substances constituting individual parts of the organism, LeDantec would be perhaps the first to renounce with joy his single individual sub-

[208]Le Dantec: Ibid. P. 294—295.

stance, similar throughout the whole organism, which as he himself states, makes histological differentiation at least inexplicable.

THEORIES OF CHEMICAL DEVELOPMENT

In his fundamental work "The Struggle of the Parts of the Organism," and therefore at a time, before Roux had yet reached the preformistic view of idioplasm or germ plasm which he later very clearly adopted, and which in many respects is like the conception of Weismann; when also he still considered development to be rather the complex result of a long series of purely chemical phenomena, and nevertheless had not yet welcomed Weismann's theory of the non-inheritance of acquired characters as a deliverance from a nightmare, at that time he sought to explain this inheritance in the following way:

First he notes that the germ plasm although it becomes separated at the very commencement of development from the organism in process of formation, "remains nevertheless dependent upon and in relation with this organism; for it must be fed and grow and multiply and to that end it receives its nourishment from its parent by chemical metabolism, and might still be influenced in its own nature in this way." [209]

He supposes further that on the one hand each structural formation may be conditioned by certain special, chemical relations, and vice versa that each variation of form which the adult organism undergoes through functional adaptation produces in its turn a certain

[209] Roux: Der Kampf der Teile im Organismus. P. 60.

special chemical change. This chemical change would later become transmitted to the germ plasm by means of the metabolism.[210]

One can not rightly comprehend here, how a special chemical modification, produced in the germ plasm by a change of form in the adult organism, can later give rise to such a development by that germ plasm as to reproduce the same change of form at the proper time in the new organism. If the chemical variation corresponding to a definite change of form were provoked by the germ plasm in the new organism only at the time when this latter reached the same age and consequently a state of being which would be the same in its entirety as that of the parent organism when this given variation of form supervened in it, and were confined to the same limited zone in which this chemical variation was produced in that parent organism, then the conception of an actual reversibility of the phenomena would not be in itself at all impossible, that is it would not be impossible that the same chemical phenomenon might provoke in the new organism the same variation of form by which it had itself been produced in the parent organism. But in our case on the contrary this chemical variation, no matter whether it transforms the whole chemical composition of the germ plasm or only a part, will commence to act upon the new organism immediately, at the very commencement of its development, and will modify therefore not merely a limited part of the cells of the organism, but all the cells without exception. How then could this same chemical change, which operates immediately at the commencement of development and conse-

[210]Roux: Ibid. P. 61.

quently upon all stages of development and upon all cells of the organism, call forth the same result as if it had come to act upon only a very definite point and at a very definite time of the development of this organism? It seems to us that we ought much rather to conclude that these results must be very different and that with them there can be no question of any similarity whatever.

This impossibility of explaining the inheritance of acquired characters by Roux's earlier theory is not limited to it alone, but pertains to all theories of chemical development in general. And the fault lies not only in the above mentioned impossibility of the reversibility of the phenomena of inheritance which we have just considered but also in a still more generally characteristic circumstance, which is likewise common to all these theories of chemical development, and which we have elsewhere already stated for other theories. And it is mostly from it that this impossibility of reversibility comes. It consists in this, that according to all of these theories as soon as the germinal substance has once given the initial impulse to development it is unable to exercise even the slightest influence upon the further course of this development. If thus the reins by which development is directed are let fall, and each bond severed which connects the changes of the soma with those of the germ and vice versa, then it is impossible to conceive how this union could later be re-established, as soon as the need was felt of transmitting to the germ and fixing in it the requisite variation, corresponding to that which appeared in the soma as the result of a new functional adaptation.

Hofmeister's theory can be considered as an especially typical example of this complete abandonment of develop-

ment to itself, which constitutes the great defect of all theories of chemical development.

This investigator believes that the chemical activity of the cell is due in general to colloidal ferments which are contained within them and of which each is destined for a special chemical process. He admits thereby the existence of numerous colloidal ferments in cells with multiple chemical processes, and he sees in ontogeny the result of a series of chemical reactions which follow one another according to the principle of fructifying causality:

"During the development of the embryo there takes place a chemical differentiation parallel with the morphological differentiation. The formation of new chemical anlagen indicates the appearance of different ferments at definite stages of embryonal development."—"One could hardly form a better idea of the chemical transformations going on during the early development of the embryo than by supposing that at first only a very small number of ferments become active, and that these transform existing material into new substance, among which proferments or ferments of another kind appear, through which the first then become annihilated, and which become supplanted in their turn by a new generation of ferments which they have themselves produced and so on until the cycle of new chemical formations requisite for the history of the race is run through. The epigenesis of form would be then only the expression of the epigenesis of chemical forces." [211]

We shall pass over the fact that all these theories of chemical development have yet to explain the connection

[211] Hofmeister: La chimie de la cellule. Revue générale des sciences; Aug. 15, 1902. P. 730—731.

between each chemical and the corresponding morphological stage of development; for this morphological character of different chemical reactions has not so far been observed in any phenomena of the inorganic world, since it has absolutely no analogue in the process of crystallization which is a property of the molecular structure of already formed, stable substances, that is of substances in perfect statico-chemical equilibrium. But we may mention the fact—and after all which has been said above no further proof of it is required—that the fundamental phenomena, such as the regeneration of amputated organs, the occasional reappearance especially in crosses of atavistic characters long since disappeared, and especially the ontogenetic repetition of phylogeny and the inheritance of acquired characters, not only find no explanation in all these hypotheses of chemical development but are on the contrary absolutely irreconcilable with them.

Darwin, Galton, DeVries, Weismann

It would be useless for our purpose to tarry especially over any one of these four theories, the underlying idea of all being the same identical conception of preformistic germs. The progressive elaboration of this idea which has proceeded gradually from the first to the last of these theories presents however the following noteworthy phenomenon. Preformistic germs, which were devised by Darwin, one could well say, chiefly for the purpose of accounting for the inheritance of acquired characters, were then deprived by Galton in great part but not completely of this property, and finally with DeVries, and still more with Weismann became themselves the greatest difficulty for accepting that inheritance.

Of Darwin's pangenesis it is necessary here to mention only the conception that the sexual or reproductive organs in general were not so much the place of refuge to which the germ plasm withdrew immediately after its separation from the soma at the very commencement of development, as rather the containers of the germinal substance continually produced and secreted by other parts of the organism lying without these organs, so that they build up as it were the sexual or reproductive cells out of this valuable material thus received and accumulated.[212]

In Darwin's hypothesis this conception of the reproductive organs as mere glands for the reception and giving up again of the germinal substance was intimately associated, although in its essence quite separate and independent, with his further conception of the free circulation of the gemmules throughout the organism; and he supposes, as is known, that these gemmules were produced and secreted continuously during the adult state by all somatic cells indiscriminately,—by those already present as well as by those just appearing in consequence of a new functional adaptation. Now if Galton by his experiments on the transfusion of blood from a rabbit of one species to the blood vessels of another belonging to a related species, has provoked a thoroughly justifiable doubt of this supposed circulation of gemmules, especially in so far as it was carried on in the blood vessels, the original idea remained nevertheless unshaken, that is that the germinal substance is assembled in the sexual glands after it has been formed in some real place of origin external to them.

[212]Darwin: The Variation of Animals and Plants under Domestication. II. P. 370, 379.

Because of the fact that the theory of Darwin derives the germinal substance from all parts of the soma rather than from one well defined region of it, its partisans could certainly not object to these experiments that they leave the conception still possible that the germinal substance might perhaps be transmitted from such a special well defined region to the sexual organs only along certain very definite special ways, which might be quite different from the blood vessels. And on account of the nature and properties attributed to the gemmules they would be still less able to advance the conjecture that a substance might possibly be reproduced at a distance, quite like another substance, by the direct influence of the latter, by means of some other means of connection of such nature that it would not require any real and proper material transmission. From this the conclusion may be drawn, that all theories which do not exclude or perhaps even include one or the other of these two hypotheses upon the manner of transmission or upon the means of reproduction at a distance of the germinal substance, are completely justified in accepting Darwin's conception of the sexual glands, acording to which the latter have only the function of receiving and accumulating a substance the real origin of which is outside these organs.

In the case of Galton we shall recall only that he was the first who introduced the theory that *stirp*,—i. e., the germ plasm consisting of numerous germs or of gemmules which remain behind after the extrusion of the particles concerned directly in the formation of the new organism—separated itself entirely from the soma immediately, at the commencement of development. Through this separation of the stirp from the soma he opened the way which later led necessarily to the uncon-

ditional rejection of the inheritance of acquired characters. Nevertheless he did not immediately venture to go so far but continued to admit as a sort of concession that in the adult organism a gemmule might occasionally escape from the somatic cell, which had produced it and was also its customary abode, even though this cell had been only shortly before acquired in consequence of a new functional adaptation; then this gemmule might be taken up by the reproductive organs and become likewise a part of the stirp and the acquired character which had appeared in the somatic cells might thus be inherited.[213]

In the case of DeVries we should remark that he assumes that the germinal substance, that is the sum total of the pangens, is present equally in all nuclei only because he, as we have also seen in the case of Driesch, took it for granted that nuclear divisions are qualitatively equal. If then a nucleus of a somatic cell acquired new pangens, as a consequence of a new local functional adaptation, then they would have to remain in the place where they arose and could not enter the reproductive cells also. And so much the more since he also asserts that the substance which will later actually form the sexual cells separate itself from the soma immediately, at the commencement of development, and passes along certain "Keimbahnen," which may be recognized, chiefly because upon them the greater part of the pangens remain inactive.[214]

In respect to Weismann we remark once again that in consequence of a more rigorous logical elaboration of the doctrine of preformistic germs, which has convinced him

[213]Galton: A Theory of Heredity. Journ. of the Anthropological Institute. January 1876. P. 342—343.

[214]De Vries: Intracellulare Pangenesis. P. 188—189.

of the necessity of regarding them as bound up with one another into a rigid structure, he has been led, through the conception of these preformistic germs which was forced upon him by particulate inheritance, to deny most energetically every possibility of the inheritance by the germ of characters which the soma had acquired by functional adaptation.

Weismann admits, it is true, that sometimes external influences acting uniformly upon the whole organism, like temperature and other such things, can alter the determinants of the soma and the corresponding determinants of the germ at the same time and in the same direction; as occurs for example in the determinants of the wing scales of the butterfly *Polyommatus phlaeas*, whose color changes as we have seen when it is transported to a warmer climate. But the cases which permit of this explanation, which resembles in many respects the above discussed diplogenesis of Cope,—the only cases which Weismann admits,—are limited by this investigator to so small a number, and are also of so peculiar a kind that it would be wrong to assert that he held less determinedly to his earlier stand as an opponent of the Lamarckian theory.

We may point out however, the following contradictions. He admits inheritance in unicellular organisms while he denies it in the pluricellular and thinks he can justify this by saying simply that as the unicellular divide always into two equal halves they need only preserve what they have acquired, in order to transmit it unaltered to the new individuals. But this is not right. For new functional adaptations acquired by the anterior end of the infusorian Stentor, for instance the acquisition of "Membranelles" by the peristome in consequence of the fusion

of several cilia, would then become transmitted only to that one of the two new individuals to which the anterior part falls in the division, and could in no wise be transmitted to the other individual in which this anterior part is formed anew. If one assumes on the contrary, that transmission goes on by means of the nuclei, and can therefore proceed equally into both of the two newly forming individuals, one could not then understand, wherein the transmission of somatic modifications in the unicellular animals, which is accomplished by means of a part of the organism containing in itself no membranelles and quite distinct from them, would differ from the transmission of any modification experienced by any organ of a pluricellular organism, which likewise goes on by means of a fragment containing no part of the modified organ and quite distinct from it. So much the more since the substantial identity of the complex unicellular with the pluricellular organisms, which we have already discussed above, corresponds also with a substantial identity in their development, as is shown by the fact that the fundamental biogenetic law of the repetition of phylogeny by ontogeny is followed in the development of unicellular animals also, as for example, in the formation of the new frontal field in the division of Stentor coereleus.[215]

And in relation to all these theories with preformistic germs from Darwin to Weismann we might mention once more the insurmountable difficulties that would be encountered if one were required to explain by them this very fundamental law, either in unicellular or pluricellular organisms. This impossibility and the fact that in the

[215]Johnson: A contribution to the Morphology and Biology of the Stentors. Journ. of Morphol.; vol. VIII, No. 3, Boston, U. S. A., Ginn, August 1893. P. 519.

end the acceptance of these germs has led necessarily to systems which reject the inheritance of acquired characters concur to prove, although more proof is certainly no longer necessary after all the other considerations which we have developed in an earlier chapter, that the very idea of these preformistic germs is untenable, as is thus every theory founded upon them.

However limited the number of theories or hypotheses selected by us, and however rapid and brief the critical exposition which we have made of them, it seems to us nevertheless that it is unnecessary to proceed further with our examination. For it has shown us that among the principal theories, which up to the present have been devised to explain the inheritance of acquired characters, none has accomplished this difficult task, and it has already served another purpose for which chiefly we undertook it. This purpose consisted on the one hand in bringing to light in other theories the most suggestive and fruitful ideas put forward; on the other hand in determining the conditions which are necessary and sufficient to render possible the inheritance of acquired characters, and a critical examination of concrete theories already developed has certainly helped to put these conditions in evidence better than simple reflection upon them could have done.

If we take a look over the road which we have thus far traveled we see that among these conditions those which have appeared to us as the essential and fundamental ones are the three following:

1. All the manifold physical, chemical, morphological, and physiologic variations, which can appear in the most different parts of the organism, are to be ascribed

to specific alterations of a single form of energy, so that the latter appears, as it were, the common denominator for these variations that are quite unlike in nature and whose combination or separation is thus permitted as often as required.

2. The determinative influence which the germ substance in its totality exerts upon the soma cannot be limited to the first moment of the first cleavage of the egg but must persist throughout the whole of ontogeny up to the adult condition, so that the germinal substance never as it were loses touch with the soma, but rather remains in a continual state of reciprocal action and reaction with it.

3. The influence exerted by the soma in this way must be reversible, that is the germ substance must be influenced in such a way that it can call forth again at the proper moment, at the numberless different points of the soma of the new organism, all the same, respective, special, somatic conditions by whose complex modes of being the germ substance itself was already influenced in the parent organism in so special a way.

This last condition which alone implies in itself the whole question of inheritance falls again into two parts. First the germ substance must be influenced always in such a way that it is capable of giving back at the required moment the same influence, qualitatively identical but in the reverse direction, which it had already experienced as the single resultant of all the elementary somatic influences to which this germinal substance was simultaneously subjected in the preceding organism. Second: the germ substance which thus gives back again the influence, by which it was influenced, qualitatively identical but in reverse direction, must be localized at a

single definite point of the organism, which is always the same, both when the parent soma exerts its influence upon the germ substance which it contains, and also when the latter exerts upon the new organism its own determinative ontogenetic influence.

It is therefore our task now to investigate in the following chapter whether the centroepigenetic hypothesis already set forth above really satisfies all these conditions and is consequently capable of really affording the adequate explanation for the inheritance of acquired characters, which we seek.

CHAPTER SEVEN

THE CENTROEPIGENETIC HYPOTHESIS AND THE EXPLANATION OF INHERITANCE AFFORDED BY IT.

As we said at the end of the third chapter, when the end of development is reached, and there comes with it a cessation of the steady activation by the central zone of new specific potential elements, there is also a cessation of the perturbing action which that zone had up till then exercised upon the dynamic equilibrium of each ontogenetic stage; so that the organism attains at that moment the final equilibrium of the adult state. But we should note that a new perturbing influence can now come into play, namely, the functional stimulus in the widest sense with all its innumerable variations.

In the same manner, we said, as the perturbing action of the central zone had formerly upset the equilibrium which was but just formed, and so provoked the passage of the organism to a new ontogenetic state, so now each lasting change of the functional stimulus by disturbing the dynamic equilibrium of the adult state, will induce another general distribution of nervous energy. Consequently each cell of the entire organism or of certain portions of the organism will now be traversed by a nervous flux which is specifically different from that before existing, and specifically different in different cells.

In each nucleus of these cells, we continued, a par-

ticular specific potential element will consequently be formed and deposited, which will be added to the element or elements already present. All these elements, new as well as old, deposited in the somatic nuclei, will, however, be lost with the death of the individual; and those alone will escape this destruction which are deposited in the germinal substance of the central zone. The lasting variation of the functional stimulus will thus have had for its total effect, in so far as the species is concerned, the simple addition of a new specific potential element to the germinal substance.

Arrived at this point, we reserved for one of the following chapters the examination of the manner in which this new element would act in the ontogeny of the next following organism. It is then with this examination that we must now occupy ourselves in the present chapter.

We should first dwell a little more in detail upon this hypothesis, which we mentioned only in passing in connection with the posthumous action, or "Nachwirkung," of the nucleus in enucleated fragments of unicellular forms. We mean the hypothesis that the substance which constitutes each specific element, and which is capable of giving as discharge a single well-determined specific nerve-current, is also the same and only substance which this specific nerve-current can in its turn form and deposit.

This should not appear so very strange to us, since the inorganic world itself presents a phenomenon similar in certain respects. The substance which actually constitutes the charge of ordinary electric accumulators is capable of giving back inversely, during its discharge, the same kind of energy which it had previously received,

and by which it had itself been deposited, namely the continuous electric current. The most important difference consists in this, that an electric accumulator is capable of restoring always only one and the same kind of energy, but not solely such or such intensity of current. It constitutes, for that reason, only a generic potential element; but such accumulators would attain the completeness of specific potential elements—receiving and restoring instruments of the greatest delicacy—if one could make it possible that each one of them should receive and restore only a single definite intensity of current. The similarities and differences which nerve currents present, in comparison with electric currents, quite warrant us in assuming in nerve currents some of the properties of electric currents, and in attributing at the same time to the first other properties which the electric do not possess, provided these qualities are not incompatible with the others.

It is known that, if we designate by E the electromotor force of an accumulator or of any electro-chemical generator, it can furnish currents of any intensity i whatever, according to the resistance R of the circuit, according to the equation $i=E/R$. Thus,—even though the terms of motor force, of resistance, of intensity, or more generally of specificity, transferred from electric to nervous currents are very indefinite—we may very well venture, nevertheless, as a preliminary trial hypothesis, to attribute to nervous currents as among the properties which they might have analogous to electric currents precisely those contained in this equation.

As it involves nothing incompatible with the properties expressed by this equation, we may imagine a nervous accumulator, constituted by a given substance

capable of being produced and deposited solely by a current of a definite intensity or specificity, and at the same time capable of producing, by its decomposition, this current only, of the same intensity or specificity i is that of the charge. This accumulator, then, will discharge itself and produce this current as often as its nervo-motive force, which we may still call E, is sufficiently great to overcome the respective resistance, according to the equation: $E=iR$.

Finally, we can assume that the magnitude of this nervo-motive force, is proportional to the quantity or mass of the substance which has been gradually deposited and accumulated, as if the successive infinitesimal deposits of this substance were innumerable little Leyden jars arranged in serial order. Then the greater the mass of the specific substance of this nervous accumulator the greater in proportion will be the resistance which its discharge will be able to overcome. At the same time, this accumulator, capable of surmounting by its current of a fixed intensity i a given resistance R, will be capable also of surmounting every other resistance less great than R; for to effect that, it will suffice that it be not the total quantity of material at disposal that enters into action, but only a portion more or less large, so as to furnish for each resistance $R'<R$, the nervo-motor force $E'<E$, given by the formula:

$$E'=iR'$$

Suppose now that the discharge of this accumulator on account of the ubication or the mode of its insertion, is able to flow only upon a definite point of a given plexus traversed along its meshes by as many currents of the most diverse specificities capable of combining one with

another and of decomposing again, and in dynamic equilibrium among themselves. (It may be remarked here that the expression "dynamic equilibrium" of a circulatory system is always to be understood in the sense of inalterability for the time in the conditions of movement at each point of the system. Thus, for example, the system of distribution of the drinking water of a city, which is fed from a given constant number of reservoirs, whose head of water is maintained always at the same height, and in which a given constant number of water taps are always open, will settle in a short time into a dynamic equilibrium in our sense, and continue in it so long as the accession of a new reservoir, for example, or the opening of other water taps does not cause the transition to a new dynamic equilibrium.)

As soon as the discharge of this nervous accumulator occurs, which can produce thus only a single definite specificity of current, and which can discharge itself upon only a single fixed point, it will necessarily effect a single very definite change in the dynamic equilibrium of this given circulatory system. And in the cases in which this change of the dynamic equilibrium requires the doing of a certain amount of work, this required expenditure of work or energy will be very definite for each discharge, and can be provided only by the accumulator itself. Consequently, in order that the discharge may take place, this quantity will have to be less than, or at most equal to, that which the accumulator can actually furnish.

But the quantity of work which each accumulator is capable of furnishing will necessarily be proportional to the mass of the substance which constitutes it. And since, as we saw, the resistance R which each accumulator with its current of definite specificity is able to surmount,

is likewise proportional to the mass of the substance of the accumulator, (because it is proportional to its nervo-motive force, which also is in its turn proportional to this mass, according to the preliminary hypothesis), then the quantity of work required to effect the change under consideration, must be regarded as equivalent to a resistance R, which opposes the discharge.

If now we assume that in nearly all cases, which come into consideration here, the quantity of work, requisite for effecting a given change in the dynamic equilibrium of the whole circulatory system, is proportionately greater the more considerable (if we may be pardoned for this much too indefinite expression) in quantity and quality this change is, it becomes at once conceivable why each specific potential element of the central zone can becomes activated only when the embryo has reached the ontogenetic stage, corresponding to the particular phylogenetic stage at which this element was acquired by the germinal substance. For then first will the change which the dynamic system of the embryo undergoes, as a result of the activation of this specific potential element, be the very least possible, and therefore usually also the only one whose resistance can be surmounted by the very weak nervo-motor force of this specific potential element.

The following general rule can thus be established:

The smaller the mass and therefore the nervo-motor force of a specific accumulator, so much the more closely is its discharge dependent upon the condition that the whole dynamic system, above all and very especially in the immediate neighborhood of the accumulator, find itself again in exactly the same state in which it was when the accumulator was formed. Conversely, the greater the mass of the accumulator, the

more easily are the conditions to be obtained which are able to permit its discharge.

Let us suppose further that as a result of external in-influences there are induced at the same moment at a few points of the system a corresponding number of new nerve currents, specifically different from the preceding, so that the system is thereby caused to pass over to another dynamic equilibrium. It is clear that there will then be deposited in each point of the system,—and not merely in those which external influences have directly modified,—a new specific potential element, in mass more or less large according to the time during which the new state of dynamic equilibrium persists. At the same time, however, all these same points of the system will preserve, in a potential state—not in activation—,all the specific elements which were desposited during the preceding state of dymanic equilibrium.

If, such being the state of things, it now happen that even any single point whatever of the system is brought back again, by any external influence, to the specificity which it had already possessed in the preceding stage, that will make it possible for the respective specific elements corresponding to that stage to come again into activity, at first in the point nearest, and then from next to next until in the most distant; for then each of these elements will find its immediate environs in approximately the same conditions as when its corresponding specific current was in activity, by which it has been deposited. It will suffice then that even a single point of a system return, through the action of external influences, to its preceding state, in order that the whole system, through the discharge of the different specific potential elements corresponding to that former stage, should resume

transitorily the whole dynamic *condition* of that stage. We have here then a phenomenon of succession or of association of nerve-currents which, as is easily conceivable and becomes even clearer later, may serve as a basis for the psychic law of succession or association of ideas.

In résumé, what we have designated hitherto by the name of *specific potential element*, and what we may henceforth designate by the name of *elementary nervous accumulator,* is then nothing else, by hypothesis, than the substance of a very small mass, deposited in the nucleus by every specific nervous current which flows through it, —a substance which adds itself to the others already present without changing them, and which is able as soon as it finds itself again in conditions of environment like those present at the moment when it was deposited, to restore the same specific current by which it was produced.

This definition and the hypothesis involved answers at once the question as to the mode of action which the new specific potential element, acquired by the germinal substance of the central zone of an adult organism in consequence of a new functional adaptation in this organism, will follow during the ontogeny of the next following organism. For from all we have thus far said, it results that this new specific potential element will first be able to become active when the embryo shall have already attained the same state in which the parent organism found itself immediately before it acquired this same new specific potential element along with the new character.

Let us consider now what happens as a result of its activation: In the parent organism there was present at first a certain circulatory system S, corresponding to the

adult stage preceding the acquisition of the new character. Then on account of an external influence acting at a given point A of this system, the specificity of the respective current was changed from *i to i′*. In consequence of that the whole circulatory system S, in order to assume a new state of dynamic equilibrium, transformed itself into a different system S′, in such a way that at another given point B, that of the central zone, the specificity of the respective current underwent a very definite corresponding variation from intensity i_1 to i'_1. If then there is now present in the embryo of the young organism the same circulatory system S of the parent organism, and if, on account of the activation of the specific potential element in question, there is produced at the same point B of this system, the same variation of specificity from intensity i_1 to i'_1, it is evident—and we shall see later that a few facts from the inorganic world prove experimentally the general principle upon which our assertion rests—that there must follow the same change as before of the dynamic equilibrium of the general system from S to S′, and that, consequently, there will now be produced at the point A the same specific modification as before from i to i′. In this way the inheritance of acquired characters finds a most complete explanation.

Let us note parenthetically, that nuclear somatization conceded, we must regard each of the substances forming the different specific potential elements of any nucleus as capable of gradually replacing the others by continual increase of its mass, when the respective specific current, on account of the incessant repetition always of only one and the same stimulus, passes very frequently through the nucleus. A nucleus thus somatized,—that is to say, one composed wholly of a single specific substance,—would

acquire in this way, on account of the considerable mass of this substance, a potential energy capable of overcoming a considerable resistance to its discharge, and would then be able to respond always in that single way only which corresponds to the single specific nervous current which it is able to activate and which constitutes its irritability, even if it be provoked to discharge by external influences or accidental stimuli which are quite different from those to which it is ordinarily exposed.

"A muscle cell," says Oscar Hertwig, "replies to every kind of stimulus by contraction, a gland cell by secretion; an optic nerve can perceive only light, no matter whether it be stimulated by light waves, by electricity or by pressure. Similarly plant cells also are endowed with their own specific energies: the reaction to stimulation receives everywhere its specific stamp from the special structure of the irritable substance, or in other words, irritability is a fundamental property of living protoplasm, but under the action of the environment manifests itself in specific reactions according to the specific structure of that protoplasm." [216]

And Claude Bernard defined irritability as: "the property of living elements of reacting each according to its nature to an external provocation or stimulus." [217]

"One conceives of the irritable substance," continues Hertwig, "as a system of material particles in unstable equilibrium, provided with forces at high tension. In such a system, a very small shock of a single particle is sufficient to put all the other particles in motion, each transmitting its own motion to its neighbor. That ac-

[216]Oscar Hertwig: Die Zelle und die Gewebe. I, P. 76.

[217]Claude Bernard: Leçons sur les phénomènes de la vie communs aux animaux et aux végétaux. P. 248, 281.

counts for the fact that a small stimulus as cause may often result in an extraordinarily great reaction, just as a grain of gunpowder kindled by a small spark may provoke the explosion of a great mass." [218]

We have opened this parenthesis on nuclear somatization and cited these passages from the two investigators in order to set in clear relief the fact that in the definition given above of the specific potential elements, both the conception of *accumulators of nervous energy in tension*, and that of *accumulators of a specific nervous energy constituting their special irritability*, are ordinary conceptions very generally employed which are expressed here in words at most only a little different from the ordinary. The only new thing which the above definition includes is the hypothesis that the substance which is thus capable of giving as a discharge a given nervous current was produced and deposited only by a nervous current of the same specificity, but in the inverse direction, and could have been produced and deposited only by such a current. But in this hypothesis, quite simple as it is, lies everything; for it is just it which alone can explain completely the fundamental law of the reversibility of the relation between action and reaction, between stimulus and impression, which governs all organic life. The inheritance of acquired characters, the psycho-mnemonic phenomenon proper, the process of specialization and somatization of the cells in consequence of which they react in their habitual manner to accidental stimuli unusual to them, even the vital phenomenon itself in all its generality, all of these, as we have seen and shall see, are only so many

[218]Oscar Hertwig: Die Zelle und die Gewebe I, P. 77.

special cases of this reversibility, and all find their immediate explanation in this very simple hypothesis.

In résumé: By this hypothesis of a nervous accumulator formed and deposited by the same specific current which it can afterward restore, the first of the two sub-conditions, included in the third condition, necessary and sufficient to account for the inheritance of acquired characters, are fulfilled. On the other side the localization of the germinal substance in the central zone, which constitutes the point of departure and the foundation for the hypothesis of centroepigenesis, has already satisfied completely the second of these sub-conditions. As to the two other conditions, the first has already been satisfied by considering the nervous current with its numerous different specificities as the common denominator or as the basis of vital phenomena of the most diverse kinds which are in activity at each instant in the most varied points of the soma; the second was satisfied by assuming a continuous action on the part of the germinal substance throughout the whole of ontogeny, by means of the steady activation of new specific potential elements pouring their discharges into the general circulatory system. It follows from this that centroepigenesis is able singly and alone to explain the inheritance of acquired characters, because it fulfills these conditions which we rightly regarded not only as necessary, but also as sufficient.

For greater clearness, nevertheless, it will be worth while to institute, as we have indicated above, a comparison between this ontogenetic development, as it would be constituted according to the hypothesis of centroepigenesis, and a very characteristic phenomenon, in some respects analogous, which is presented by the inorganic world. The reproduction of a sentence by a phonograph

is, in fact, if the expression be allowed, a true centro-epigenesis. The needle placed at the center of the membrane repasses through all the stages through which it had passed when the sentence was spoken; and each of these stages was only the total effect of the repercussion upon this point of all the extremely complex vibrations called forth in the membrane by external influences, in this case the vibrations in the air. Since the needle,—one single point of the dynamic system,—repeats thus the same identical series of specific movements which were before produced at this point by the concurrence and union of all the complex movements of the system, these successive specific movements of this one point are thereby again decomposed into all the same successive complex modes of the entire dynamic system, in this case constituted by the extremely complex vibrations of the membrane.

Let us suppose, moreover, that it were possible to interpose in an ordinary telephone wire transmitting a series of variations of the electric current a complex accumulator capable of receiving the current and of returning it after a certain time just as it was in its successive variations. Then the whole series of complex dynamic systems, which were formed by the successive complex vibrations of the membrane receiving the spoken words could be reproduced, just as at the receiving station, after any interval whatever, exactly as with the phonograph. Well, the role which centroepigenesis attributes to the germinal substance is fundamentally nothing else than that it forms a similar complex accumulator.

Finally it may appropriately be noted here, that this comparison with the phonograph permits us to make still more definite and clear all that we stated at the end of the fourth chapter, namely that the centroepigenetic

hypothesis is able to explain particulate inheritance completely, without requiring the help of any preformistic germs whatever. Concretely: let us imagine two exactly similar phonographs, and let us have the same singer render the same melody in exactly the same way first before one then before the other. Only let us suppose that one hears at a certain moment during the second song, for example, one of the audience cough, or a door slam, or clapping of applause. Obviously both phonographs now will reproduce the same melody in the same way, with the single difference of the accessory noise, which will not destroy in the slightest the otherwise complete conformity of the two phonographic reproductions. Thus we have here an actual and characteristic case of particulate inheritance for the production of which it is mechanically sufficient that the series of successive specific vibrations of the middle point of the membrane differs from the corresponding series of vibrations in the other phonograph only through a single vibration or through a very inconsiderable group of these specific vibrations.

From the explanation which centroepigenesis gives of the inheritance of acquired characters there follows also at once a very important consequence. If we mean by functional stimulus not so much the external influence as rather the immediate modification induced by it in the vital process, then the functional stimulus according to the centroepigenetic hypothesis is of quite the same nature as the ontogenetic stimulus. And this appears to be indicated also by the best demonstrated facts.

We regard it as absolutely necessary to understand first clearly this distinction between external physical actions and functional stimulus. For the former do not themselves constitute the true and proper functional

stimuli, but they do determine them. External influences and functional stimuli are two special forms of energy, the first of which can transform itself into the second, but they are fundamentally different from each other. The one is inorganic, the other biologic and vital in nature. And the designation "functional stimulus" properly applies to the external action, in so far as, and at the moment when, it transforms itself into vital energy. The possibility of a substantial identity between the functional stimulus and the ontogenetic stimulus can obviously exist only in case the former is understood in this way.

That being disposed of, it becomes worth while to recollect that Roux distinguishes embryonic life and adult life as two things of totally different nature: "In the life of all parts (of the organism) two periods must be distinguished: an embryonic period in the widest sense in which the parts develop, differentiate, and grow of themselves, and an adult period in which growth, and in many parts indeed, the complete replacement of material used up, goes on only with the co-operation of stimuli. These stimuli might thus give origin to something new which, if it were produced in this manner throughout several generations, would become hereditary, that is, be formed without these stimuli in the descendant, and become thus in our sense embryonal." [219]

These two periods characterized respectively by embryonic differentiations and by functional changes are regarded by Roux, as we have said, as essentially different: "Since the changes going on in adult men, are produced only by means of external transforming influences,

[219]Roux: Der Kampf der Teile im Organismus. P. 180—181.

whereas embryonal differentiations, on the other hand, take place without or almost without such differentiating stimuli, there is reason to believe that these results are produced in another way which, while undoubtedly controlled by natural laws, is nevertheless for the time incomprehensible by us. Consequently the essence of embryonic differentiation and its immediate physico-chemical causes are for the moment quite inaccessible to us." [220]

Centroepigenesis, on the contrary, teaches us, as we have seen, that embryonic and functional differentiation are essentially the same. And in support of this view we may recall among others the following principal orders of facts:

"All the organs which fulfill their specific function already in the embryo have there a life dependent upon stimulus (Reizleben) in proportion to this function." [221] This indicates that an organism in process of development may be at one and the same moment in the embryonic period in respect to some of its parts and in the functional period in respect to other parts, without ceasing for that reason to behave in all its manifestations as a whole of a thoroughly individual nature.

A number of characters begin to develop embryonically which later require the help of the functional stimulus to complete their development: "In embryonic development some parts are ontogenetically formed and developed to a certain grade of functional capacity, which have been formed phylogenetically entirely by functional adaptation. Functional stimuli seem to be necessary only for that remainder of development which belongs from its

[220]Roux: Ibid. P. 166.

[221]Roux: Der Kampf der Teile im Organismus. P. 182.

essence to functional life proper." [222] This would speak for the gradual accomplishment of the transition from the embryonal to the functional period without any sudden and precipitate change, and so speaks also for a gradual, hardly noticeable replacement of the ontogenetic stimulus by the functional so that one must suppose the two stimuli to be active simultaneously and in combination.

So Hyrtle, having cut across the motor nerves of the muscles of one side of the face of a new born rabbit, stated that a year after there was not only atrophy of the muscles but the bones of that side of the head had undergone a surprising arrest of growth. He attributed this arrest to the fact that "after muscular paralysis there was lacking the traction and compression, which provoke living parts of the bone to activity and cause the normal growth of the bone." [223]

Alesandrini and E. H. Weber similarly found in monsters "that in the absence of the anlage of the spinal cord there were lacking in the corresponding nerve territory both the nerves and the muscles and that the bones and joints belonging to these were abnormally formed, the latter being in part rigid." [224]

It may be remarked here that as some of these parts had attained a certain development even without the functional stimulus, and during the very period in which normally they would have had the co-operation of the functional stimulus, it is therefore clear that if there had

[222]Roux: Zur Orientierung über einige Probleme der embryonalen Entwicklung. Zeitschrift für Biologie. Bd. XXI; München, July 1885, P. 503. Gesammelte Abhandlungen, II, P. 231—232.

[223]Oscar Hertwig: Die Zelle und die Gewebe. II, P. 175.

[224]Roux: Der Kampf der Teile im Organismus. P. 51.

not been this pathological absence of this latter, the ontogenetic stimulus and the functional would have co-operated at the same time in the same formation. Therefore one cannot, as we have said, be oblivious of the indication that this harmonious and parallel co-operation of the two stimuli, in combination with the fact that in no embryonic structure whatever is there to be demonstrated any substantial difference in the manner of formation and development between the purely hereditary portion due to the ontogenetic stimulus alone, and the portion due to the functional stimulus, is strongly in favor of the essentially identical nature of these two stimuli.

Finally a number of organs which would attain their complete development through the ontogenetic stimulus alone, have their development hastened by the accidental intervention before the proper time of the requisite functional stimulus. Thus, for example, in prematurely born children the visual sense develops earlier; that is to say its development is accomplished in a total number of days, counting from the first instant of development, that is smaller than the ordinary number such as would be given by the time of ordinary gestation augmented by the number of days necessary for the infant born at term to acquire the same degree of development of sight.[225] And this demonstrates again, that the functional stimulus can replace the ontogenetic stimulus, or better, that it can co-operate with it and add itself to it, thus strengthening its effect; a thing which would be difficult to conceive of were the two stimuli of different nature.

To these facts of the most general character, we can

[225]Roux: Der Kampf der Teile im Organismus. P. 182.

add further the following more special ones which are quite similar in their nature to the preceding.

The tails of larval amphibians, cut off obliquely in respect to their axes, become regenerated in such a way that the axis of the regenerated fragment is always perpendicular to the plane of section and forms consequently a certain angle with the axis of the stump. Nevertheless, all these tails, because of regulative forces within the organism, tend gradually to straighten themselves. Now Barfurth has demonstrated that in frog larvae which are prevented almost entirely from swimming by putting them in shallow water divided into a number of small compartments by water plants, this straightening goes on in a much less complete manner and much more slowly than in those which are placed in deep water and which are thus able to swim freely. That is a proof that functional adaptation of the tail to swimming co-operates with the entire action of the internal regulative capacity, or in a wider sense with the ontogenetic stimuli, and adds itself to them, intensifying and accelerating their action.[226]

An example of the ontogenetic stimulus having not yet replaced the functional, or better, being not yet endowed with a quantity of potential energy sufficient to overcome by itself the resistance which opposes its activation, and which has therefore need of this functional stimulus in order to commence to act, is furnished us by the axolotls. These tailed batrachians can retain their external gills indefinitely and live out their lives and reproduce their kind with external gills, or be transformed into amblystomae, according as they are or are

[226]Barfurth: Versuche zur funktionellen Anpassung. Arch. f. mikrosk. Anatomie, Bd. XXXVII; Drittes Heft. Bonn, Cohen 1891; especially P. 403—405.

not prevented from passing at the proper moment of their development to terrestrial life. "One could say that this depends upon the amblystomal form being not yet sufficiently fixed in the heredity of the species, since the epigenesis resulting from this heredity does not yet necessarily cause the appearance of the amblystomal form so long as the conditions to which this form is adapted are not realized." [227]

Finally the experiments of Cunningham on the colors of flat fishes already quoted above, are well known. He has shown that during their first metamorphoses, while the pigment is still present on both sides, the action of light artificially reflected upon the side of the fish which is turned toward the bottom does not prevent the pigment from disappearing even then from that side, so that in this case the color passes rapidly through a retrograde development. But a prolonged exposure to light provokes the reappearance of the pigment on the lower side, and the pigment spots are in every respect like those which are normally present on the upper side of the fish.[228]

In this experiment then one has a clear and direct instance of a functional stimulus reinforcing the ontogenetic stimulus. We say "reinforcing" because the fact that the spots now appearing on the lower side are like those above, demonstrates that they are not produced de novo by the functional stimulus, but even now depend upon the ontogenetic stimulus, which, with the help of

[227]Le Dantec: Traité de Biologie. P. 403-404.

[228]Osborn: The hereditary Mechanism and the Search for the unknown Factors of Evolution. Biol. Lect. at the Mar. Biol. Lab. of Wood's Holl, Summer Session 1894. Boston, U. S. A., Ginn, 1896. P. 91.

the functional stimulus acquires anew the power which it once had possessed in the ancestors of the existing species:—another proof that the functional and ontogenetic stimuli can act at the same time, that their actions can be added together, and that they must consequently be of the same nature.

We can then draw the following conclusions:

1. The essential similarity of the two stimuli, ontogenetic and functional, the reality of which the facts which we have just cited and a thousand others like them permit us to deduce, combined with the fact that external influences, upon which alone the functional stimulus depends, are generally lacking during the embryonal period, is sufficient even by itself to justify us in concluding that ontogenetic stimuli are nothing else than the reactivation and restitution of the functional. It constitutes thus at the same time a new argument in favor of the inheritance of acquired characters.

2. This conception of development based upon the essential identity of the functional stimulus and the ontogenetic stimulus, and up till now at least only this conception, makes it possible to explain the ontogenetic facts without presupposing in any of the stages of development any phenomenon which is not a normal physiological phenomenon, of the very same nature as those manifested by the organism in the adult state. And it thus indicates that the whole of life, at every moment of it, preserves an absolute unity in its nature.

3. Ontogeny finally appears to us in this way simply *as a continual functional adaptation, by the embryo, to the successive active modes of being of the central zone of development.*

Having thus set forth and explained the way in which

centroepigenesis is able to account for the inheritance of acquired characters in general, the particular case of this inheritance, constituted by sexual dimorphism and by polymorphism in general, which up till now we have been compelled to leave aside, becomes explained at once.

The question of primary and secondary sexual characters, writes Delage, is connected with one of the most important questions of general biology: "When one part develops in a certain way another part develops correlatively in a certain way, and if the first had developed in another way, the development of the second would also have been different; and this although no direct connection exists between these two parts. The question presents itself also in the following way: In what way and under what form can this reciprocal influence of the organs acting at a distance be effected without any similarity between cause and effect?" [229]

The explanation which the centroepigenetic hypothesis can afford for sexual dimorphism is the following: It is due to the fact that in the whole series of germinal specific potential elements there are found interpolated two distinct groups of these elements, such that the activation by the central zone of one of these groups would preclude the activation of the other and vice versa. Then as soon as the two sexes have commenced to differ somatically even a very little from each other, every later sexual character, whether principal or secondary, acquired by functional adaptation by the male or female, or better the entire conformation of the whole organism resulting therefrom, would become represented in the central zone of that organism by a corresponding small group of

[229]Delage: L'hérédité etc. P. 184—185.

specific potential elements. And these could become activated in the next following organism only when the general distribution of its nervous energy should find itself in the same conditions as at the time when this new sexual character was acquired: a thing which requires above all that the organism be of the respective sex.

In harmony with this the ordinary facts of embryonic development teach us that as soon as the sexual organs of one of the sexes become indicated, the accessory organs just forming of the other sex cease to develop and remain rudimentary, while the organs proper to the sex which is already declared, both the essential and the secondary, develop completely. There is thus an arrest of growth in some organs from the fact of the development of the others, which makes one suspect that the conditions of environment created by this development of some organs hinder the further activation of energies which cause the production of organs of the other sex.

Thus there always remains latent the possibility, that the characters of the other sex may also appear in an individual already developed in the opposite way, especially in advanced age, when with the cessation of their respective functions all the sexual organs and characters lose their vitality; a thing which often occurs in many species and in man himself, and which occurred particularly in that famous old hen which Darwin has reported, which after having ceased to lay eggs took on not only the voice, but the plumage, the spurs, and the fighting temperament of the cock.

One can say the same of polymorphism. In fact this also can very well be regarded as dependent on an inter-

polation, quite analogous to that of which we have spoken above, of three or more groups of specific potential elements in the whole series of germinal elements, with the result that the activation of one of these groups prevents that of all the others. Thus each form of the polymorphous kind would have its own characters which arise entirely by the inheritance of characters acquired through functional adaptation.

It is nevertheless to be remarked that a few forms of certain polymorphous species are possibly to be ascribed also to the circumstance that a few groups among all the specific potential germinal elements of the entire series are hindered in their activation, not so much by properly ontogenetic conditions which depend upon the development of other characters, as rather by quite general conditions of temperature, nutrition, etc., so that thus the form in which these groups are not activated, differs from the principal form only through the absence of some single character. This might be the case, for example, in the working bees and generally in the neuters of many insects, the explanation of which would thus be quite similar to that which Spencer gives in his polemic with Weismann. But evidently these forms with incomplete development represent essentially only a special case of the preceding supposition.

We can thus say also that the fundamental principle to which centroepigenesis has recourse in order to explain sexual dimorphism and polymorphism in general, that is, to explain how it comes about that the development of certain characters prevents that of certain others which remain latent, is still the same principle which has already served to explain the fact that ontogenetic

characters present themselves exactly in the order of their phylogenetic acquisition.

If the capacity which centroepigenesis possesses of explaining the Lamarckian principle extends so far as to account, without needing any subordinate hypothesis, for the inheritance of those characters also which either sex has acquired separately and at different times and each on its own account, it shows itself still more especially and completely adapted to explaining the inheritance of those characters common to both sexes as well as those belonging only to one sex which, in consequence of their excessive complexity and of the circumstance that they are located not simply in definite parts of the organism but rather in numberless places at the same time, have so far always constituted the greatest difficulty for every theory which has attempted to explain the inheritance of them. We refer to the instincts.

It is evident in fact that we can regard every instinct as due to a special relative mode of being of the different psychic centers and of the nervous network connecting them. For it depends upon this relative mode of being that to certain definite sensations which arrive at certain perceptive centers there correspond necessarily certain reflex movements induced by the motor centers which are in definite communication with these perceptive centers. Now, however, every deposition of new psychic centers, perceptive or motor, mnemonic or volitional, and every new connection of these by means of nervous communications more or less direct or indirect, more or less conductive or resistant, would be, according to the centroepigenetic hypothesis, only the effect of as many special modes of being of nervous circulation in the limited territory of the nervous system alone. It

is therefore easy to imagine, above all if we recollect that the central zone would be just one part,—the least differentiated part of this system, that for each one of these complex modes of being of the nervous configuration constituting a given instinct there must correspond in the central zone itself its respective specific potential element, and this latter becoming active later in the next following ontogeny as soon as the general nervous configuration again becomes like that which was present at the moment immediately preceding that in which this element was formed in the parent, must be capable of so modifying this configuration as to make it acquire the same instinct which the nervous configuration of the parent had acquired by the action of external influences.

If now we draw a conclusion from all that we have said thus far, we can very well assert that the attempt to account by means of the centroepigenetic hypothesis, for the Lamarckian principle in all its manifold and comprehensive manifestations has not failed. One notes also that this hypothesis can be assigned to the class of mnemonic theories of heredity, but with this important difference, that the theories of Haeckel, Hertwig, Orr, Cope, and other similar ones, in order to explain the phenomenon of the inheritance of acquired characters appearing during development, have recourse to a phenomenon still more special and more complex, the mnemonic, and therefore do not and cannot constitute any real explanation. Centroepigenesis on the contrary, as we saw utilizes as subordinate hypothesis a very general and very simple biological phenomenon, which in many respects indeed is like certain phenomena of the accumulation of energy in the inorganic world, and

which would be at the same time the basis of both the phenomenon of heredity and the mnemonic phenomenon. So that these latter instead of being explained by each other, would both be explained by this single phenomenon, more simple and more general than either.

So it will be worth while for us, in the last chapter which follows this, to subject the mnemonic phenomenon to a rapid examination in order to see if it likewise really finds an adequate explanation in this supposed elementary biological phenomenon of a specific accumulation of energy. And then we shall examine more closely the question whether this same hypothetical elementary phenomenon cannot at the same time explain at least partially the fundamental properties of the vital phenomenon itself in all its generality.

CHAPTER VIII

THE PHENOMENON OF MEMORY AND THE VITAL PHENOMENON

The comparison between the phenomena of development and the phenomena of memory especially after the discovery of the fundamental biogenetic law, that ontogeny is a recapitulation of phylogeny, has presented itself spontaneously to a large number of authors. "The germ," said Claude Bernard, "seems to preserve the memory of the organism from which it came."[230] Haeckel attributes development to the mnemonic quality of his plastidules. We have seen in the sixth chapter how Orr endeavored to explain the recapitulation of phylogeny during ontogeny by the mnemonic law of habit; how Cope held that ontogeny is called forth by the unconscious memory of phylogeny; how Nägeli and in some places, Hertwig himself, attributes to the idioplasm the faculty of remembering, so to speak, the successive stages through which it had gradually passed.

But by far the boldest contender for the acceptance of the essential likeness of the ontogenetic and mnemonic phenomena has been Hering: "What else is this reappearance in the developing daughter organism of characters of the parent organism, than a reproduction,

[230]Claude Bernard: Leçons sur les phénomènes de la vie communs aux animaux et aux végétaux. P. 66.

on the part of organized matter, of processes in which it already took part at another time, even if only as a germ in the ovary, and which now at an opportune moment it recalls exactly while reacting to the same or similar stimuli in a way similar to that formerly followed by that organism of which it was once a part, and whose vicissitudes it then had shared? If the parent organism by long custom or repeated action has changed somewhat in nature in such a way that the germinal cellule within it has also been affected however feebly it may be, and if this latter commences a new existence growing and developing into a new being of which the different parts are yet only itself and flesh of its flesh; and if in thus developing it reproduces that experience which it had already shared at another time as part of a great whole; this is indeed just as astonishing as when the memory of his earliest childhood suddenly comes back to the old man, but it is no more astonishing. And whether it is still the same organized substance which reproduces a process already once experienced, or whether it is only a descendant, a portion of itself, which in the interval has grown and become large, this is manifestly a difference of degree only and not of essence." [231]

We shall not repeat here the objections which have been advanced against the similar affirmations of Orr

[231]Ewald Hering: Über das Gedächtnis als eine allgemeine Funktion der organisierten Materie. Wien, Gerold, 1876. P. 16—17. Hering's thesis has recently been taken up again by Richard Semon and been treated more thoroughly and completely in his work: Die Mneme als erhaltendes Prinzip im Wechsel des organischen Geschehens. Leipzig, Engelmann, 1904. (See Eugenio Rignano: Une nouvelle théorie mnémonique du développement. Revue Philosophique. Paris, Alcan, November 1906. No. 11.)

and Cope. Only it may be noted once again that the absence of any analysis, however conjectural, of the nature of the phenomena of memory makes the explanation of development which Hering tried to give in this way, not only quite indefinite and nebulous, but also gives it the appearance of a quite artificial comparison between processes much too unlike.

The same is true in a yet greater degree of the general theory of Hering of which development is a particular case, and which considers memory a general function of all living organized matter. Ribot accepts this theory and modifies it in that he expresses the view that "memory is essentially a biological phenomenon and only accidentally a psychological one." [232]

This extension of the mnemonic faculty over every vital phenomenon without exception, though it contains much truth, cannot by itself constitute any explanation of either one phenomenon or the other, but rather helps to plunge both into greater obscurity; for while by this comparison the obscure fundamental peculiarities common to both become in no wise clearer, one loses sight of those most familiar and characteristic properties which are different in the two phenomena, and which are the ones which have served to give, up to the present day, the most correct idea possible of both.

The mnemonic phenomenon can serve then neither as an explanation of the phenomena of development nor of vital phenomena in general, because it is as we said a phenomenon even more special and more complex than those which it has been summoned to explain. Nevertheless there may yet be the possibility that the resem-

[232]Ribot: Les maladies de la mémoire. Paris, Alcan, 1901. P. 1.

blance which appears to exist between some of the essential properties of these three phenomena may be explained by a still more general and more simple phenomenon which would form the common basis of all three categories of phenomena; the ontogenetic, the mnemonic properly so called or psycho-mnemonic, and the vital.

We have already shown that this common phenomenon might perhaps be implied in the hypothesis set forth above, in which we regarded the specific potential elements as accumulators of specific nervous energy or as *specific elementary accumulators.* In just this capacity of restoring again the same specificity of nervous current as that by which each element had been deposited one would look for the cause of the mnemonic faculty in the widest sense, which all living matter possesses. And further the very essence of the mnemonic faculty would consist entirely in this restitution.

It may be remarked here that the *specific potential elements* which as we saw in the preceding chapter could be called also *specific elementary accumulators* are thus susceptible now of receiving a third name, namely that of *mnemonic elements.*

According to this definition, ordinary electric accumulators, which are as we saw merely generic accumulators, represent, one may say, only very imperfect mnemonic elements. On the contrary the more capable they were of storing up each a single one of the innumerable minute specific variations of such an energy and of reproducing it identically at each discharge, the more perfect mnemonic elements they would become.

As of all the vital phenomena the psycho-mnemonic are those which present most distinctly the mnemonic

faculty possessed by all living substance, it is in them that we shall be able best to verify the laws which become impressed upon this mnemonic faculty through the conception that it is based upon the specific accumulation and reproduction suggested above. And the most important of these laws have just been briefly outlined in the preceding chapters.

Of the three elements of memory: the preservation of certain states, their reproduction, and their localization in the past, Ribot thinks that the first two alone are necessary and characteristic.[233] We can note, that the hypothesis of mnemonic elements permits us to conceive of this preservation of certain states as an accumulation of specific energy and their reproduction as the discharge of that specific energy.

"When we speak," writes Maudsley, "of a trace, or vestige or residuum all we mean to imply is that an effect is left behind in the organic element, a something retained by it which disposes it to a similar functional act; a disposition has been acquired which differentiates it henceforth, although we have no reason to think that there was any original specific difference between one nerve cell and another."[234] This something which leaves an impression after it in the nerve cell and which disposes it to other similar functional acts will be to our mind, a true and real material residue of substance capable of reproducing the same functional current as that by which it had been deposited. And the differentiation of nerve cells, as indeed of all other somatic cells, consists in the acquisition by each of them of a

[233]Ribot: Ibid. P. 2.

[234]Maudsley: The Physiology of Mind. Third edition. London, Macmillan, 1876. P. 270.

greater or less number of specific or mnemonic potential elements differing from one cell to another. But we must bear in mind that this differentiation is not acquired exclusively after birth, but appears already within certain limits, at least in relation to all the congenital instincts, during ontogeny.

"We see," writes Hering, "how an entire group of sensations become reproduced with such vividness and in such precise order of space and time that it can deceive us as to its reality. This shows us in a most striking way that even after the sensation and perception in question has long since disappeared, there remains still in our nervous system a material trace, an alteration of the molecular or atomic connections by which the nervous substance is rendered capable of reproducing these physical processes, with which the corresponding psychic process of sensation and perception is also determined."—"The representations do not last as representations but what does persist is that particular attunement of the nervous substance, by virtue of which when it is properly struck it sounds again today the same note which it gave forth yesterday." [235]

This conception of Hering of the disposition of the nervous substance to sound again the tone of yesterday is derived from the physical phenomenon of acoustic resonators. The nervous substance which would be made to vibrate in a given specific way at a given point by a definite elementary sensation or representation would remain from that moment capable of vibrating always and exclusively according to that specific mode. According to the hypothesis of mnemonic elements on the contrary,

[235]Hering: Über das Gedächtnis etc. P. 8, 9.

it is well to repeat again, each elementary sensation or representation would consist not so much in a specific vibration of the nervous substance at this or that point as in the production by the action of external stimuli of a given specific nervous current. In this way the memory of an elementary sensation or representation would consist only in the reproduction, by the action of causes now internal, of the same specific nervous current. In other words the way in which the hypothesis of mnemonic elements or specific elementary accumulators would conceive of the mnemonic phenomena is as follows:

A series of sounds or of words, for example a certain melody, or some phrase of a discourse, when once it has entered by the ear, we can imagine, produces a series of nervous currents in the auditory nerve specifically different from one another, just as in a telephone the successive electric currents are specifically different from one another (in this particular case different in intensity) which the same series of sounds produces in the receptive apparatus and later transmits along the wire. If then one or several nerve centers, after receiving these specifically different currents, are capable of storing up these specific energies, each distinct from the other, and to reproduce them unaltered later at the moment of discharge, and if, further, the discharge of each immediately preceding specific energy and it alone is capable of producing the liberation of the specific energy immediately following, (and we have seen above that this is one consequence of the hypothesis of specific elementary accumulators), it will be in this way possible for the same succession of different ideas or impressions to be

repeated a great number of times and it is in just this that the mnemonic phenomenon consists.

One could evidently say the same thing of the optic phenomenon, that is to say, of any series of colors or specific luminous vibrations which succeed one another in space or time.

Ribot has rightly said that "There is not one memory, but memories; that there is not one seat of memory, but particular seats for each particular memory." [236] And, according to our theory, each mnemonic element would just constitute a particular seat for each elementary sensation or each particular specific impression.

In this sense also, that is to say on the condition that the expression "nervous elements" be not disjoined from the conception of elementary specific accumulators or mnemonic elements, we can accept the idea of memory which this investigator (Ribot) has put forward: "If we attempt," writes he, "to conceive a good memory and to express this in physiological terms, we must figure to ourselves a great number of nervous elements, each modified in a particular manner, each taking part in one combination and probably capable of entering into several. Memory has then static and dynamic bases. Its strength is in relation to their number and stability." [237]

"It has been asked," continues Ribot, "if each nerve cell can preserve several different modifications or if once modified it is forever polarized. The number of cerebral cells being about 600,000,000 according to the calculations of Meynert (and Sir Lionel Beale gives a much higher figure) the hypothesis of a single impression

[236] Ribot: Les maladies de la mémoire. P. 11.
[237] Ribot: Ibid. P. 32.

is not inconceivable." [238] It may be remarked here that according to the hypothesis of mnemonic elements there is room in each brain cell for a whole series of specific deposits and not merely for one specific deposit. Indeed we must suppose, as we have seen, that the germ substance contains a very great number of specific potential or mnemonic elements, and we can also assume that the same is true of the very complex mnemonic centers.

Provisionally it can be affirmed that the close dependence of memory upon the nutritive processes,[239] indicates strongly that the preservation of memories is to be ascribed to accumulations of substance. Further, as was very well remarked by Hensen, the fact that many memories may remain entirely dormant throughout several years, and then can come again with great distinctness into consciousness, notwithstanding that all the parts of the organism have been renewed several times in the interval,[240] indicates, (if one recollects that assimilation consists in the incessant reproduction of new masses, always of identically the same substance), that in order to preserve these memories it is sufficient if for one given substance there be substituted another identical one.

If it appears thus to be shown by facts, that the preservation of memories is due to accumulation and conservation of substance, a whole series of other facts seems to demonstrate that the reawakening of these memories consists in the restitution of the same currents as had formerly constituted the actual sensation or impression.

[238] Ribot: Ibid. P. 17.

[239] Ribot: Ibid. P. 155—163.

[240] Hensen: Über das Gedächtnis. Kiel, Universitäts-Buchhandlung, 1877. P. 13.

We need not recall here all the innumerable examples which show that the motor or secretory or in general the physiological effects of the mnemonic reawakening of a given sensation or impression are quite identical with those of the real sensation or impression: for example, the recollection of a certain dish produces the same salivation as is provoked by the dish itself; the memory of the beloved person can cause each time the same reddening of the countenance, the same brightening of the eyes, the same acceleration of the pulse as the direct view of that person; every time that a mother thinks of her nursing child there comes a flow of milk into the breasts.[241] These are some examples which show the substantial identity of the functional and mnemonic stimulus.

Here we should like to cite just the following experiment of Wundt mentioned by Ribot: "If, after looking for a long time at a picture with very vivid colors, we keep the picture before our minds with the eyes closed and after that suddenly open the eyes and fix them upon a white surface, we see there the picture which we had kept in our minds, but in the complementary colors. This fact, remarks Wundt, proves that the nervous operation is the same in the two cases, in the perception and in the memory." [242] According to our view this indicates that the nerve current which corresponds to the color, let us say red, of the picture, and reproduced, together with all other currents corresponding to the other special characters of this picture, by the mnemonic center recalling it again, is equal but opposite in direction to that current which the red rays coming from the white

[241]Lewes: The physical basis of mind. P. 288.
[242]Ribot: Ibid. P. 11.

surface send toward the center: Consequently only the currents sent by complementary rays from this white surface can reach that center, and these combined with the currents corresponding to the other characters of the picture must give it the same aspect as before only with a complementary color.

If the preservation of each memory is due to deposits exactly equal in number to the specific elementary nervous currents which the sensation or complex impression had provoked in the nervous system, we are then in a position to comprehend also the phenomenon known under the name of *abridgment*. "Every memory," says Ribot, "however clear it may be, undergoes an enormous abridgment. The farther the present recedes into the past, the more do the states of consciousness diminish and disappear. Reviewed at several days distance there remains little or nothing of them; for the most part they have darkened into a nothingness from which they will never again emerge and have taken with them the time duration inherent in them. Consequently a diminution of the states of consciousness is a diminution in time." [243]

This disappearance of the elementary states of consciousness producing the abbreviation of memory will be due then, according to our view, to the disappearance of the secondary mnemonic elements, that is to say those provided with a minimum quantity of the respective substance, (and of the potential energy which is the consequence of it), from the series which constitutes the entire memory. Possibly this disappearance can be caused by the fact that the nutritive fluid has come

[243]Ribot: Ibid. P. 44, 45.

gradually to be entirely absorbed by the principal mnemonic elements of the same series and by the new elements which later supervene as a consequence of later sensations also stored up in memory.

Let us note that this abridgment of every memory, interpreted as above, becomes then completely capable of explaining also the similar abridgment which phylogeny undergoes during ontogeny. In fact, of the ancient mnemonic elements constituting the germinal substance, the most pronounced, that is those which are represented by the largest quantity of substance, will alone persist. The less pronounced ancient mnemonic elements, the total quantity of nourishment for all mnemonic elements remaining the same or varying only within definite limits, will have all their portion of nourishment taken away by the more pronounced ancient mnemonic elements, and by the new mnemonic elements whose number will continually increase with each phylogenetic advancement. Not being able consequently to regain their substance completely in each ontogeny they will gradually disappear.

If we have always supposed so far, as the first degree of approximation necessary to the comprehension of the fundamental nature of the phenomenon, that ontogeny reproduces phylogeny entirely, these abridgments of memory permit us then to penetrate still farther into the inner nature of this phenomenon and to recognize that ontogeny instead of being an entire reproduction of phylogeny can be only a succinct recapitulation.

In recalling a given memory the mnemonic cells do not lose the "impression" as we call it which they preserve of that memory; on the contrary the more a memory is recalled the more the respective "impression"

is reinforced. This signifies that the activation of mnemonic elements or the performance of their function merely causes their mass and their potential energy to increase. This fact, that the active participation of the mnemonic centers in the biological phenomena of memory leaves them unaltered in the same state as before, so that they are just as capable and even more capable than formerly of reproducing many more times the same phenomena, reveals them to us in this relation also as entirely similar in nature to the germinal substance, which active participation in the biologic phenomena of ontogeny leaves likewise in the same state as before and even renders always more capable of again producing the phenomenon of ontogeny.

According to the centroepigenetic hypothesis the mnemonic elements of the germinal substance, with the exception of the last belonging to the adult stage, can become active only at each new ontogenesis; that is their reawakening would take place only after long periods of repose which might last even through several years. Such reawakening of mnemonic centers at long intervals of years constitutes a very ordinary phenomenon. Cases are frequent, for example, of adults who are able to repeat poetry which they had learned in their earliest childhood, even after many years during which they have never had occasion to repeat it at any time. Coleridge speaks of a young girl who, in the delirium of fever, repeated long pieces in the Hebrew tongue which she did not understand, but which she had heard read aloud a very long time before by a priest in whose service she had been.[244] A Lutheran preacher of German origin

[244]Maudsley: The physiology of mind. P. 25.

living in America who had in his congregation a considerable number of Germans and Swedes related to Dr. Rush that nearly all a little before dying pray in their mother tongue. "I have," said he, "innumerable examples of it and among them several in which I am sure they had not spoken German or Swedish for fifty or sixty years." [245]

The following two facts are still more typical:

A lady in the last stages of a chronic disease was taken from London to the country. Her little daughter, who had not yet learned to talk, was sent to her and after a short visit was sent back to the city. The lady died several days later. The daughter grew up to maturity without remembering her mother. She had then occasion to see the room in which her mother died. Although ignorant of that fact, upon entering the room she started, and when asked the cause of her emotion, she said "I have a distinct impression of having been in this room before. There was in that corner a lady in bed, apparently very ill, who leaned over me and wept." [246]

Similarly, a man of very marked artistic temperament, as soon as he came in front of a castle in Sussex had an extremely vivid impression of having already seen it, and he recalled in his imagination the procession of visitors in all its details. He learned from his mother that he had actually been brought there on an excursion at the age of sixteen months and that the recollection which he had of the visit was very exact.[247]

These examples show then how remarkable can be

[245]Ribot: Les maladies de la mémoire. P. 146—147.
[246]Ribot: Ibid. P. 143—144.
[247]Ribot: Ibid. P. 144.

the persistence of conditions latent in memory. Let us note further, that these last two cases present in a very striking form one of those "revivifications of memory through contiguity in space," as Ribot would call them.

This reawakening of memory through contiguity in space is only a particular case of the general law of the association or succession of ideas. They indicate that the mnemonic center becomes active only when the sight of the same place induces in the environment of that center almost the same state of distribution of nervous energy as was present at the former time when it received the impression. That is exactly, as we have seen in the preceding chapter, the immediate result of the hypothesis of specific elementary accumulators there advanced.

In the mnemonic phenomena properly so called, it is the infinitely diverse and constantly changing conditions of the outer world and the corresponding sensations following in the individual which call forth like a phantasy such and such an association or succession of ideas. But in the development of the embryo which is removed from the action of every external perturbing influence and above all, which is provoked by the activation of different specific germinal elements from one and the same complex mnemonic center constituted by the germinal substance, the succession of mnemonic states of this latter called into activity one after the other and of the corresponding stages of ontogeny must inevitably proceed in an uninterrupted series, always the same for all individual ontogenies of the same species. For to reawaken each mnemonic element of this germinal substance there must again concur exactly and exclusively those conditions of distribution of nervous energy in

the embryo which had been provoked by the reawakening of the mnemonic element immediately preceding.

It is then in development even more than in mnemonic phenomena properly so called that there operates the law of rigorous succession, in which, as Ribot says, each member of a series "suggests" the following.[248]

In summing up all that we have said thus far we can thus affirm that if the mnemonic phenomena, properly so called, cannot serve to explain ontogenetic phenomena nor the latter to explain the former, their resemblance which has nevertheless been noted by so great a number of authors can be explained by a third phenomenon more general and more simple than either. And this phenomenon consists in the faculty possessed by all living substance of accumulating and giving back again individually the different particular specificities of generic nervous energy, which constitutes the essence of all vital phenomena whatever.

* * * * * * *

This property of accumulating and giving back specific nervous energy, attributed by hypothesis to all living organic substance, is thus shown to be capable of explaining the most fundamental biological phenomena, from histologic specialization of cells which respond always in their customary specific manner no matter how unusual may be the stimulus which excites them, to the inheritance of acquired characters, from the evolution of species and the repetition of phylogeny by ontogeny, direct consequences of that inheritance, to mnemonic phenomena properly so called.

It remains for us to demonstrate that this property,

[248]Ribot: Les maladies de la mémoire. P. 8.

as we have affirmed before, can help to explain in great part the essential character of the vital phenomenon itself in all its generality—that is assimilation.

The fact that strikes us first of all is, that the vital phenomenon depends upon continual reproduction, for assimilation constantly reproduces the substance which is gradually consumed. It is to be expected therefore, that if there are any fundamental properties of living organic substance which explain the phenomena of development or of reproduction in general, they must then be capable of accounting for assimilation also, inasmuch as it is itself a phenomenon of reproduction.

That being granted it will be worth while that we next stop for an instant to take a look at and consider briefly a few of the principal conceptions which biologists have put forward on the nature of either the vital phenomen or of assimilation, and which are of the greatest interest from our point of view.

Roux, for example, rightly urges that the nature of life must be dynamic. "Life is in its essence a process, and cannot therefore have a static definition. It is therefore only a processive and consequently functional definition which can approximate the essence of organic life." [249]

On the other side we have already seen the reasons for concluding that the essence of the vital phenomenon consists in an activation of nervous energy. We recall that according to Orr for example, the fundamental property of living substance is an "elemental nervousness." [250]

[249] Roux: Über die Bedeutung der Kernteilungsfiguren. Leipzig, Engelmann, 1883. P. 18. Gesamm. Abhandl. Bd. II. P. 142.

[250] Orr: A Theory of Development and Heredity P. 86.

We have already seen also that Claude Bernard, in agreement with that, considers the sensibility of the nervous substance as nothing else than a particular modality of irritability, which would be a general property of all living substance. "Sensibility," writes he, "considered as a property of the nervous system, is only a higher degree of a simpler property which exists everywhere in all living substance both animal and vegetable. It has nothing essential or specifically distinct. It is the special irritability of the nerve just as the property of contraction is the special irritability of the muscle, and as the property of secretion is the special irritability of the glandular element. These phenomena are so many different degrees of one and the same elementary phenomenon." [251]

Bard also remarks that if the nature of the energy constituting the basis of all vital phenomena must be single, the infinitely varied modalities which the same vital phenomena present must then be due to as many corresponding modalities of this single energy.

"In spite of the complexity and multiplicity of physiological functions," he writes, "it is possible to refer them fundamentally to a general function of the living cell, namely the function of producing derived substances. Cellular specificity can be explained and made comprehensible only as this single function is able to insure the innumerable functions necessary for an entire organism. The variety of derived substances is itself the effect and the proof of the radically different vital properties of the kinds of cells which create each of them."

"It is necessary to establish an essential difference

[251] Claude Bernard: Leçons sur les phénomènes de la vie communs aux animaux et aux végétaux. P. 289—290.

between the physico-chemical properties of the derived substances created by the specific activity of each living cell, and the properties of the cell nuclei which spring directly from the special forces which constitute life. The specific differences result from the very modality of the cell life. Cell life is a special property of matter which, like all its highest properties, undoubtedly consists in a particular mode of movement. One can say in some measure that the cell is a circuit of life. Further vital force, like light or electricity, with which one can compare it, not so much to show that it is very similar to them as to facilitate the comprehension of it, presents multiple varieties due to variations of wave lengths, of their rythm, direction, or of any other element of this movement which one could suppose or discover. These variations are without doubt incomparably more numerous than those of electricity, which are limited enough, than those even of light, which are certainly infinitely more numerous. And just as colors indicate the differences of the different kinds of light, so the different physiological functions of species of cells indicate different modalities of life." [252]

It is worth while to stop a moment here, to show in this connection how readily biologists are inclined to fall into two opposite exaggerations.

Some deny flatly the possibility of ever arriving at an understanding of the nature of life. But if we ask ourselves in what this understanding of the nature of life could consist, from the point of view of positive philosophy, we have no difficulty in recognizing that

[252] Bard: La spécificité cellulaire et ses principales conséquences. La semaine médicale. Paris, 10. March 1894. P. 116.

such an understanding must be reduced to comparing vital phenomena with some physico-chemical model already known, suitably modified by the particular special conditions imposed upon it so that just these special conditions shall determine the differences which exist between this vital phenomenon and the phenomenon of the inorganic world most closely related to it. If this be so, it is then the duty of science emphatically to reject such a denial of scientific thought as the renunciation of the quest of this understanding would constitute. Whether one clearly recognizes it or not, it is just this search for the nature of the vital principle which properly constitutes the principal object and the final goal of all biologic study in general.

Others again are not willing to accord to life even the slightest property which should not be simply physico-chemical in nature. Among all these it is enough to cite the example of Verworn who not only relegates assimilation to the category of purely chemical phenomena, by means of his "Biogen" hypothesis, but who would explain protoplasmic currents, the protusion of pseudopodia, the movements of cilia, and in general all movements of living beings by a double and alternative chemotropism of protoplasmic substance rather than by currents of nervous energy. Protoplasmic substance, in fact, according as it remains unstimulated or is stimulated, that is, partially decomposed by the stimulus which would agitate it mechanically, would possess a chemical affinity for the oxygen of the environment or for the substances produced by the nucleus capable of rebuilding the partially decomposed protoplasmic substance. And to this alteration of different affinities, the opposite proto-

plasmic movements of expansion and contraction would correspond.[253]

Now it is evident that this endeavor not to attribute to vital energy any specific nature of its own, and consequently to explain even the most characteristic phenomena of life by means of only those energies which physics and chemistry afford us to-day, can have no more success than as if one should attempt to explain chemical phenomena by means of physical phenomena only. For the conception that the form of energy on which vital phenomena are based is different from all forms of energy which have hitherto been observed in non-living bodies, has absolutely nothing unscientific in it, any more than the conception, for example, that electricity may also be a form of energy different from all others.

Vital energy, nervous energy, we admit at once, will certainly be a particular case of the more general physico-chemical forms of energy already known or yet to be known, and as such it must necessarily be subject to the laws which control these latter; and also, a fortiori, to the laws which control all energy in general. But even as such, that is as a particular case of more general, physico-chemical forms of energy, it will have besides further special laws of its own which are only experimentally to be determined and cannot be deduced from the more general laws even though it must always be subjected to them. And it is just these laws of its own which, out of a physico-chemical energy, make it vital energy. This conception has led us to attribute to nervous energy, set forth as the basis of life, special

[253]Verworn: Die Biogenhypothese. Jena, Fischer, 1903; and Die Bewegung der lebendigen Substanz, especially P. 100—103.

properties, which electric energy, in certain respects related to it, does not possess.

If, passing on now to assimilation, we examine the conceptions which the biologists have formed of it, we shall see that their opinions on that subject are quite remarkably concordant.

Thus, for example, Lewes says: "The peculiarity of vital processes consists in this, that living matter undergoes molecular changes of composition and decomposition which are simultaneous, and by this simultaneity it preserves its integrity of structure."[254]

"Life," remarks in his turn Oscar Hertwig, "manifests itself, expressed in the most general terms, in this that the cell, by virtue of its own organization and under the influences of the external world undergoes continual changes and develops forces whereby its organic substance, on the one hand continually destroyed with determined manifestations of energy on the other hand is regenerated."—"The life process depends then, on a continual destruction and reformation of organic substance."[255]

But the clearest and most suggestive of all is Claude Bernard in the following celebrated passage:

"The characteristics of life considered in their essence and in their entirety can be classed in two groups."

"1. The phenomena of consumption, of vital destruction, which correspond to the functional phenomena of the organism."

"2. Plastic phenomena or phenomena of vital crea-

[254]Lewes: The Physical Basis of Mind. P. 5.

[255]Oscar Hertwig: Die Zelle und die Gewebe. Bd. I, P. 54, and Bd. II, P. 190—191.

tion, which correspond to functional repose and to organic regeneration."

"Everything which goes on in the living being is in relation to one or other of these types; and life is characterized by the union and combination of these two orders of phenomena."

"Disorganization or dis-assimilation uses up living material while the organs perform their functions. Assimilative synthesis regenerates the tissues. It reassembles the reserve materials which the functioning organism must use up. These two processes of destruction and renovation, although inverse, are absolutely connected and inseparable, in the sense at least that destruction is the necessary condition of renovation. The phenomena of functional destruction are themselves the precursors and instigators of the renewal of material by the formative process which is accomplished silently in the interior of the tissues." [256]

Dastre remarks finally that "Claude Bernard developed from the analysis of substances excreted as the result of physiological work, his conviction that every manifestation of functional phenomena is necessarily associated with some organic destruction. For excretions certainly bear witness of organic demolition."

"But the underlying reason," continues Dastre, "of this interdependence between chemical destruction and function is made recognizable by energetics. A part of the organic material (reserve material, but also living protoplasm) becomes decomposed, chemically simplified, reduced to a lower degree of complexity, and abandons

[256]Claude Bernard: Leçons sur les phénomènes de la vie communs aux animaux et aux végétaux. P. 125—127; 157; 347—348.

in this descent the chemical energy which it enclosed within it in the potential state."

"Every act which gives out energy, which produces heat, or movement, every manifestation whatever, which can be regarded as a transformation of energy, necessarily consumes energy, and this is borrowed from the substances of the organism. The functioning muscle produces heat and movement, the functioning of glands produces heat, the functioning of nerve and brain produces a small quantity of electricity and heat. All these manifestations of energy rest upon a destruction of organic matter, a chemical simplification as the source of the energy manifested. In this way material destruction not only coincides with functional activity but is the measure and the expression of it."

"The reconstructive synthesis of protoplasm is on the contrary a phenomenon of evident synthesis, of a certain chemical increase of complexity. Its formation at the expense of simpler nutritive materials requires then an appreciable quantity of energy."

"The phenomena of living beings," continues this author, "may be divided into two categories. Some are intermittent, alternative, and are produced or accentuated at certain times but cannot be continuous. These are functional processes. There are others in which this property of sudden and intermittent expenditure of energy does not appear at all. They are in general nutritive processes. The muscle which contracts, functions. It has an activity and a repose. During this apparent repose one could not say that it is dead. It has life and this is here obscure in comparison with the manifest activity of the functional movement."

"The phenomena of functional activity are those

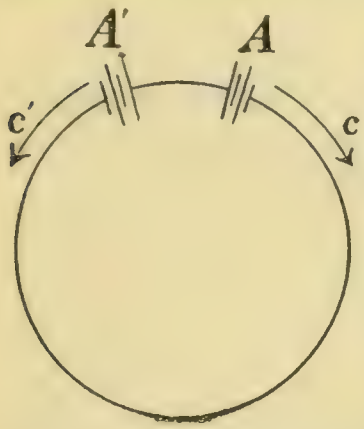
which catch the eye and by which we are inclined to characterize life. These are conditional on processes of consumption, of chemical simplification, of organic destruction through which energy is set free. And it is quite necessary that it should be so, since these functional manifestations expend energy. These phenomena in which the vital activities are most apparent are the least specific. They have only the character of general phenomena."

"The phenomena which accompany functional repose correspond to the reconstruction of the reserve materials destroyed in the preceding period, to organic synthesis. This remains in the words of Claude Bernard, 'internal, silent, hidden in the expression of its nature, reassembling silently the materials to be expended. We never see these phenomena of organization directly. Only the histologist, the embryologist tracing the development of the element or of the living being notes the changes, the phases which discover to him this homely work, here a deposition of material, there the formation of a membrane or a nucleus, yonder a cleavage or a folding, or a renovation.' This category of phenomena is the only one which has no direct analogues. It is peculiar to the living being and limited to it. This developmental synthesis is the true vital phenomenon. Life is a creation." [257]

It is then this reconstructive synthesis of living matter which goes on during the so called functional rest which we must seek to explain through the properties which we have postulated above for nervous energy taken as the basis of the vital phenomenon.

[257]Dastre: La Vie et la Mort. Paris, Flammarion, 1902. P. 103, 107, 208—209, 210—211.

For this purpose let us suppose in conformity with the hypothesis set forth above that one could construct an elementary electric accumulator capable of furnishing a single given intensity or specificity of current and that its electro-motive force or difference of potential between the poles is proportional to the mass of substance constituting its charge; as if each new increment however small of this mass constituted an element by itself which would be added in serial order to the others.



Let us consider two of these accumulators, A and A′, inserted with their poles inverted in the same circuit. Suppose they are quite identical, except that the one, A′, is entirely without charge, and the other, A, has its full charge. Let us suppose now that the current, c, generated by A which tends to charge A′ can under certain circumstances cause an oscillatory discharge, i. e., a continuous oscillation of the current, now in the direction of c, now in the contrary direction c′, and that certain external alternating currents could induce in the oscillating circuit sinusoidal electro-motive forces of the same frequence as this oscillating discharge and thereby strengthen the sinusoidal electro-motor force of the latter which at the beginning was determined by the original difference in charge of the two accumulators A and A′.

Then with each half oscillation the one accumulator will become more strongly charged in proportion as the other discharges, and there will be produced as a final result of the series of oscillations a consequent continual increase of the total mass of the two accumulators A and A′, as long as the saline solution serving as their common aliment is not insufficient.

If the amount of electro-motive force contributed by the induction current at each oscillation is proportional

to the amount of electro-motive force which is directly dependent upon the difference in charge between the two accumulators existing at any moment, if for example, it represents a definite fraction of the latter, and thereby will gradually decrease in amount as this difference between the two charges becomes less with each oscillation, then both the amount of this difference and that of the induced electro-motive force will sink to nothing after a certain period of time, theoretically infinitely long, practically more or less short, which we can call the period of reconstitution or of replacement of material consumed.

As soon as the charges of the two accumulators have become equal there will take place no more provocation of oscillating currents and the total mass of the two accumulators whose increase had become always smaller and smaller will now not increase any further at all.

But if at this instant either of the two accumulators, suddenly becoming inserted, aside from its own oscillating circuit, into another circuit, discharges into the latter wholly or partially, then the difference between the respective charges of the two accumulators will again be present and the former process of oscillation will begin again. And this will result again in the increase of the total mass of the two accumulators above the amount which it had already reached before this last discharge. We can compare this discharge of one of the two accumulators outside the circuit of oscillation with the nervous nuclear discharge outside the nucleus into its surrounding protoplasm or its environment in general, that is with the biological functional excitation which produces the same trophic effect.

Further if at the moment when the two accumulators have arrived at the condition of equality between their

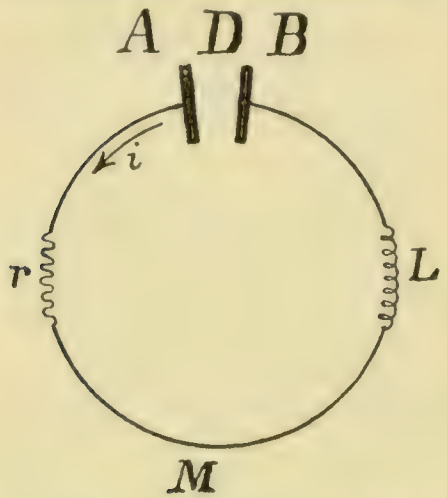
respective charges and so of repose, one of them instead of becoming discharged into another circuit, becomes replaced by a third accumulator whose charge is different from the other two now equalized charges, the result will be the same. And the impulse given to the process of oscillation will be greater the greater the difference between the charge or electro-motive force of the new accumulator and of the old one replaced. In other words, to make use of biological expressions: the rejuvenescence of the specific potential elements formed by the pair of accumulators will be proportionally greater, the more quantitatively unequal are the two half elements which have become thus mutually fecundated.

If we substitute for the conception of electro-motive force that of nervo-motive force, our hypothesis concerning the nature of the vital process in each specific potential element will consist simply in supposing that the latter is comparable to this pair of accumulators inserted with inverted poles in the same elemental oscillating circuit, which we would call intra-nuclear circuit, but in which there enters into play instead of the alternating electric induction current, general thermal energy in the same way.

Assimilation, the new formation of living substance, would then be dependent, according to the hypothesis, upon a kind of oscillatory charging and discharging flux, upon a kind of intra-nuclear oscillatory discharge which becomes provoked by the extra-nuclear or functional nervous discharge in consequence of the disturbance of the equilibrium between the nervo-motive forces of the two accumulators opposite each other. The vital element would thus be conceived of as only a double specific

elemental accumulator of nervous energy in continual charge and discharge.

As will be noted we have here a phenomenon in some respects similar to the electric resonators of Hertz, in which an electric discharge caused by the difference of potential existing between the two armatures of a condenser, is transformed into an oscillatory discharge. It will be appropriate here to indicate briefly in just what this phenomenon consists.



Let A and B be the armatures of a charged condenser which are suddenly connected with each other by an external conductor, ArMLB, in such a way that the latter makes a circuit open only at the point D of the di-electric. In the accompanying figure r represents the total resistance of the circuit, and L the inductance or coefficient of self induction of this circuit. When the capacity c of the condenser and the inductance L of the circuit are in a certain relation to each other, and r is small, we can get an oscillatory discharge which forms as it were a sinusoidal alternating current; that is the electricity oscillates from A toward B and from B toward A, with a frequency determined by the inductance L and the capacity c. If we cause the resistance r of the circuit to become constantly less by employing wires of constantly increasing thickness, we approach the boundary at which this oscillation will be able of itself to continue indefinitely.

If in this case, where r is very small, we excite in the circuit by induction sinusoidal alternating electro-motive forces of the same frequence as in the oscillatory discharge, then there will arise in A and B differences of very many volts even though the number of volts so induced is small.

Upon this principle depends, as is well known, the

celebrated experiments of Hertz, which in turn have formed the point of departure for wireless telegraphy.

It is known also that such an electric resonator has been rightly compared to a vibrating dynamic system, to a pendulum which has an oscillation time of its own, to a sounding chord which the smallest impulses having the same frequence as itself can set in vibration, even in strong vibration. What happens in it is a continual periodic transformation of energy. At the instant when the sinusoidal alternating current reaches its maximum intensity, one has the maximum of actual energy, while the condenser, on the other hand, possesses then no potential energy whatever. At the instant when the intensity of the current drops to nothing, the condenser shows the greatest deformation of the respective dielectric, and possesses thus a potential energy fully equal to the actual energy possessed by the discharge at the moment of its greatest intensity, the process being thus exactly the same as in a pendulum in which potential energy is transformed continually into actual and vice versa.

It will be sufficient here, for the purpose of a remote comparison, to note the fact just indicated that a sinusoidal alternating electro-motive force induced in such an electric resonator, which need amount only to a very few volts, provided that it be of the same frequency as the oscillating discharge, will be able to induce in A and B differences of tension which may amount to many volts. For if we assume in the current so oscillating the faculty of depositing in each of the armatures of the condenser infinitely small particles of substance in series one after the other, so long as the total of their mass and the consequent electro-motor force does not surpass the electro-

motor force in the opposite direction, which this current possesses at this point and at this moment, then it will not be difficult for us to conceive of the case in certain respects analogous, which we have assumed for oscillating nervous discharges, in which the calorific oscillations, which replace here the oscillations of the induction current, continually increase the mass of living substance which will in this way be "assimilated."

Let us note that in the case of nervous currents we must assume that their specificity is constant even during the oscillation. Then the duration of each nervous discharge, and hence of each oscillation also, in cases where the specificity i of the nervous current is something dynamically equivalent to the intensity of the electric current, will likewise be definite and constant for every given specificity.

For let us consider again an electric current. If its intensity i persists for a time t, the total actual energy furnished during the whole of this time by this current will be Eit, where E represents the electro-motive force. But this total energy will necessarily be proportional to the mass M of the substance whose decomposition during the time t has produced this current; one has thus $Eit=hm$, where h is a coefficient of proportionality, dependent solely upon the units of measure selected. But if the supposition which we have accepted for nervous currents in general holds good also for this electric current, namely, that the electro-motive force is proportional also to the mass of substance which tends by decomposition to produce the current, then also $E=km$, where k again is a coefficient of proportionality dependent likewise solely upon the units of measure which are adopted.

Consequently the above equation would take on the following form:

$$km.\ it = hm,$$

that is:

$$it = h/k = H,$$

where H again is another coefficient of proportionality and dependent solely upon the units of measure already fixed above, and so represents an arbitrary, constant numerical value. It follows from this that *it* is constant. And if i in its turn is likewise constant for each specific current, t must also be constant; i. e., to each definite specificity of current, i, will correspond a likewise determinate and constant duration of discharge.

If then, no matter what conditions may induce the different discharges of a current of the specificity i, all these discharges can have invariably only the same duration t, and if this holds also for those which constitute the oscillating discharge, then the oscillation itself, which consists of a double discharge of which each one has a direction contrary to that of the other, as we stated above, will have necessarily a very definite and constant period of its own which corresponds each time to the particular specificity i of its respective current.

It follows that among all the infinite vibrations of the different rays from any calorific source whatever, there will be certainly present also those which have the same oscillatory period as the mnemonic element in the way of reconstituting itself, and those synchronous rays will then be able to give to the oscillating discharge of the latter an impulse which will be added to that received through the difference in potential of the pair of accumulators, and thus to have identically the same effect as that which the sinusoidal-alternating, electric, induction cur-

rent has upon the electric resonator with an equal period of vibration. And this becomes so much the more plausible since Maxwell's theory, of which it is scarcely necessary to remind any one, and which was wholly confirmed by the Hertzian experiments, has demonstrated the essential identity of these electric, induction oscillations across the di-electric formed by the air, with light and heat vibrations in general. The only difference consists in the period of vibration which in both the latter is much more rapid than in the former.

So we can understand how thermal energy, whether that which comes from the irradiation of the sun and from the outer world in general, or that which is developed from chemical processes of decomposition and oxidation taking place in the interior of the organism, can, in as far as it is composed of heat rays of the most different periods of oscillation, constitute the general external stimulus which activates indifferently all the vital processes of synthesis:

Let us note that to each specific discharge, to the intra-nuclear oscillating as well as to the extra-nuclear functional there will correspond very definite substances of dissimilation, for the different specificities of the nervous currents can be due only to the decomposition of substances likewise different. And even if the diversity of these extremely complex and unstable substances consists only in the different number and different mode of grouping of the same atoms of the principal elements which constitute all organic substance, nevertheless the respective substances of dissimilation to which each of these complex substances will give rise, will necessarily be different from one another. These substances of dissimilation, definite and peculiar for each specific dis-

charge, will in their turn afford, by their entire or partial oxidation, products of excretion and secretion quite definite and differing from one cell to another. These products, in their turn, thanks to their peculiar physico-chemical properties, will imprint upon the protoplasm or cytoplasm a corresponding physico-chemical character and a corresponding morphological structure. So it is conceivable how the *ensemble* of the mnemonic elements constituting a given nucleus can determine its own protoplasm or cytoplasm both from the purely physico-chemical and from the properly morphological point of view.

We arrive thus at a constant double correlation between the cytoplasm, the species of nuclear excitation, and the substance of the nucleus. For the nuclear substance will determine directly the specificity of the corresponding nervous current and its rhythm of charge and discharge; and this specificity of current thanks to the substances of dissimilation to which it will give rise, will determine the respective cytoplasm. Conversely, the specificity of the current or its peculiar rhythm of charge and discharge, once determined by the functional stimulus, will determine the substance of synthetization or nuclear substance, as also the substances of dissimilation of which the cytoplasm is constituted.

Let us summarize what has been said. The specific potential elements which have presented themselves in the preceding chapter as specific elementary accumulators, and at the beginning of this chapter as mnemonic elements, appear now as specific vital elements, that is as the smallest possible particles of organic substance capable of life. At the same time the denominations *potential* element, and *vital* element, which might at first have appeared incompatible with each other, if the

adjective *potential* had indicated a vital non-activity at that time, become entirely compatible in consequence of the hypothesis which we have just set forth. For according to this hypothesis, the element would be potential in so far as each of the two coupled accumulators would be able to furnish at need its proper extra-nuclear functional nervous discharge, and it would at the same time be conceived as in a *vital* process by reason of the intra-nuclear oscillating discharge, which continues incessantly between the two accumulators. Vital energy could thus present itself in three distinct modes: (1) In the potential, properly so called, which expresses itself in the phenomena of actual suspension of life or lethargy in its widest sense; (2) In the oscillatory potential or the intra-nuclear oscillating discharge, which constitutes the essence of the period of so called "functional repose," "organic reconstitution" of materials afterwards to be consumed, "assimilative synthesis," or "vital creation;" (3) Finally in the actual proper, or the extra-nuclear non-oscillating discharge, which constitutes the period of "excitation," "functional activity," "wear and tear," "consumption of material stored up in the rest period," "disassimilation," or "vital destruction."

As conclusion of our exposition let us note very briefly that also for three others of the most fundamental phenomena associated with vital activity this hypothesis upon the nature of life presents at least the beginning of an explanation. These are: rhythmicity, a characteristic property of all life phenomena; the phenomena of fecundation and rejuvenesence in general; and nuclear division with its characteristic and remarkable details.

A whole series of facts forces us to the opinion, that

rhythmicity should be reckoned among the most general characteristics of the modes of manifestation of vital energy. Apart from the fact that nearly all, and perhaps all external physical stimuli, from the thermal and luminous to the acoustic, are characterized by vibrations; and the other fact, a consequence of the first, of the physiological action exercised by all the rhythmical or periodical manifestations of the most diverse energies, we see that a more or less manifest and more or less regular periodicity is a fundamental character of all or nearly all biological functions. One thinks at once, for instance, of the synchronous rhythm of all the peristomal cilia of an infusorian,—a rhythm which manifests itself in the two parts of an animal which has been divided, provided these parts remain connected by a bridge of protoplasm; of the rhythmicity present in the protozoa in general, present even within the cells, shown by the pulsation of contractile vacuoles, which empty and refill themselves continually at regular intervals; of the beat of the heart, even independent of its connection with the nervous system; of the similar pulsations of the whole vascular system, the entire breathing apparatus, the uterus, and of many other organs; and finally of the periodicity of a whole series of physiological variations, which animals and plants undergo as a result of corresponding variations of the outer world, but which persist unaltered for some time even when the outer world, or the periodicity of its variations, may have changed.

Now it is not difficult to conceive of this rhythmicity or periodicity which nearly all biological functions present, as a consequence more or less direct or indirect of the vital phenomenon in all its generality, when this

phenomenon, be it only in so far as a phenomenon of assimilation, is itself essentially a rhythmic phenomenon.

In regard to fecundation we know that it was Spencer who first recognized what has been more or less explicitly accepted by others, that it consisted probably in a perturbation of an equilibrium which tended toward a stability unfavorable to vital activity.[258]

Now we have already seen how our hypothesis set forth above is able to make at once conceivable in what this equilibrium unfavorable to vital activity may consist. According to this hypothesis, it would consist in the equalization toward which the masses, and the corresponding potentials, of the coupled accumulators of each mnemonic element would tend, and which they would eventually attain, and this equilibrium would be disturbed by the substitution for one of these accumulators of another specifically equal to it but differing in mass and potential. And it is precisely in this function of fecundation, of replacing in each couple one of the specific accumulators by another differing quantitatively as widely as possible, that we find an explanation of the fact that the rejuvenation of the germ and the consequent vitality of the progeny to which fecundation tends, are proportionally greater when fecundation occurs not between individuals too closely related but rather between individuals which belong indeed to the same species but are somewhat dissimilar.

According to the same hypothesis, this equilibrium could also be deranged by the extra-nuclear discharge of one of the two coupled accumulators, and this is just what

[258]Spencer: Principles of Biology. I, P. 340—341, and II. P. 614—616.

is demonstrated by the universally known experiments upon the rejuvenescence of the infusoria, by which it appears that this rejuvenescence can be re-acquired even without any need of the ordinary fecundating conjugation, simply by causing some change in the surrounding conditions of life, and thereby provoking a strong renewal of the functional activity of the animal.[259]

Let us note parenthetically that if oscillating discharges take place between the corresponding separated specific accumulators or half mnemonic elements of the egg and spermatozoon respectively even when the egg and the spermatozoon are still relatively distant from each other, i. e. before they could coalesce into a single fecundated nucleus, we can then understand how the space between each pair of these elements can and must function just as the deformed di-electric between the two armatures of the condenser of an electric resonator, and thus be constrained to produce the attraction of each spermatic half element to the corresponding half element of the egg. And this would have as a final result an energetic reciprocal attraction between the egg and the spermatozoon.

The real cause of the sexual attraction of the two germs, male and female, would then reside in their capacity of vibrating in unison. Conversely the absence of all attraction between ovum and spermatozoon belonging to animal or vegetable species too different in kind would be due to the fact that the one germ is constituted by potential half elements of which too many are specifically

[259]Compare e. g. Hartog: Problems of Reproduction: Conjugation, Fertilisation and Rejuvenescence. The Contemporary Review, July 1892; esp. P. 94—95, 100—102.

completely different from those of the other germ, and consequently they are incapable of vibrating together with the same rhythmicity.

Finally as to indirect or karyokinetic cell division, let us admit that, when each of the two coupled accumulators, in consequence of the continual increase of its mass attains too high a potential, the two halves of each of these accumulators will tend to repel each other, just as would for example, the two halves of a conducting sphere or disc, charged with too great a quantity of static electricity of the same sign.

If we admit at the same time, that the separation of the two halves of each accumulator would break the circuit of oscillation, as would seem indicated by the rupture, retraction, and disappearance of the meshes of the nuclear reticulum during mitosis, and thus suspend abruptly the oscillating discharge, then the actual energy of this discharge still in activity at that moment will become transformed into potential energy, and discharge itself upon the first little bit of substance, or centrosome, most capable of receiving it. Consequently, without pretending thus to be able to penetrate into the smallest details of this phenomenon, we understand nevertheless how the vital phenomena of *dynamic* order, which are due to the oscillating nervous discharge, must then necessarily be followed by phenomena of *static* order, like those which are characteristic of the karyokinetic cell division.

We limit ourselves here to recalling only:

1. Delage's observation that in indirect division the longitudinal splitting of the chromosomes or of the nuclear filament begins before achromatic filaments are present which are capable of exerting upon them any pull

whatever, which warrants the inference that it is repulsion which operates between the two halves.[260]

2. Hanseman's observation, that during karyokinesis all the peculiarly vital functions of the cell, as assimilation, secretion, etc., etc., are completely suspended.[261]

3. Watase's observation, according to which the centrosome in reality is only a simple cytomicrosome but of greater circumference and greater force of attraction, and that the cytomicrosomes which always lie at the meeting point of three or more cytoplasmic fibers likewise are nothing else than small temporary clumps quite aspecific which form anew in each cell division from the contracting substance of the cytoplasmic fibers themselves.[262]

4. Ziegler's experiment, in which the poles of the horseshoe magnet took the place of centrosomes and acted upon iron dust strewn upon a thin horizontal wax plate upon which previously pieces of iron wire of forms similar to that of the chromosomes had been placed, and in which figures were obtained which were similar to those presented in nuclear division, which is a direct proof of the conception already advanced by Roux, that in the attraction exerted by the centrosomes upon the chromosomes there are in play static energies of nature similar to that of magnetic force or of static electricity.[263]

[260]Delage: L'hérédité etc. P. 149—150.

[261]Hansemann: Studien über die Spezifizität, den Altruismus und die Anaplasie der Zellen. P. 10.

[262]Watasé: On the nature of Cell-organisation. Biol. Lect. at the Mar. Biol. Lab. of Wood's Holl, Summer Session, 1893. Boston, U. S. A., Ginn, 1894. P. 92—93; und Origin of the Centrosomes, Ibid. Summer Session 1894; Ginn, 1896. P. 282, 285.

[263]Ziegler: Untersuchungen über die Zellteilung, Verhandl. der Deutschen Zoolog. Gesellsch., Leipzig 1895. P. 78—83. — Roux:

Conclusion

As the reader who has followed us thus far has already noted, there are three new hypotheses or three new fundamental conceptions which we submit to the judgment of biologists and of positive philosophers in general. Although they support one another mutually and all rest upon the same general idea of the vital phenomenon, they are, nevertheless, independent of one another, especially the first two are independent of the third.

The first is the hypothesis of centro-epigenesis to which we, as was said in the preface and explained in the first chapter, were led by the fundamental biogenetic law of the repetition of phylogeny by ontogeny with all its more or less mediate or immediate results.

The second hypothesis is that according to which each specific nervous current deposits a very definite substance which, in its turn, is capable of provoking again exclusively the same specificity of current as that by which it was itself deposited. This idea has enabled us on the one hand with the aid of the centro-epigenetic hypothesis to explain directly the inheritance of acquired characters; and has on the other hand by itself alone afforded the immediate explanation of all the mnemonic phenomena in the widest sense of the word, from histologic specialization, in consequence of which the cells answer always only in the same accustomed way to the most different accidental stimuli, up to the psycho-mnemonic phenomena or phenomena of memory properly so called.

Über die Bedeutung der Kernteilungsfiguren, Leipzig, Engelmann, 1883, P. 18, Gesamm. Abhandl. Bd. II, P. 142. — Marcus Hartog: The Dual Force of the Dividing Cell, Part I: The Achromatic Spindle Figure illustrated by Magnetic Chains of Force, from the Proceedings of the Royal Society, B, Vol. 76, 1905, especially P. 555—559.

The third hypothesis attributes the vital phenomenon essentially to an intra-nuclear oscillating nervous discharge; and this idea has enabled us, with the help of the above mentioned second hypothesis of specific accumulators, to explain likewise the fundamental property of the life phenomenon, which consists in assimilation.

It is hardly necessary to state that the first and second hypotheses although, as we have said, all the three hypotheses support each other mutually, are yet totally independent of the third, and therefore can stand equally well whether the latter is accepted or rejected.

We do not venture to offer this latter as a true and proper hypothesis. The phenomenon of life is still too little established for so bold a venture. We consider it only as a provisional scheme of the vital process which may serve as an initial concrete basis for further investigation into the nature of life. For in affording provisionally any firm foundation upon which the discussion of a question still awaiting solution can be based, one attains always the great advantage of determining exactly the conditions of the question, of showing clearly the untenability of certain views which was not possible formerly while the question had yet too indefinite a form, and of bringing us in this way slowly but certainly nearer to a correct understanding of the phenomenon, in proportion as after discarding the untenable propositions the tenable stand out more clearly and convincingly and thereby are given a more firm foundation.

It remains then only to await quietly the judgment of the critic and to express in advance our thanks to all those who are willing to accord us friendly support in word and deed, and thereby make possible a somewhat more thorough elaboration of the subject which we were

able here to handle only too cursorily. We should be especially grateful to those who along with their criticisms and objections would be good enough to send us word of any new facts which can be adduced either in support of any of our three hypotheses, or in opposition to them.

APPENDIX

ON THE MNEMONIC ORIGIN AND NATURE OF AFFECTIVE TENDENCIES.[1]

If we observe the behavior of the various organisms from the unicellular up to man, we see that a large number of their processes, and especially the most important ones, may be regarded as manifestations of a tendency of the organism to maintain or to restore its "stationary" physiological state (to use the term of Ostwald's energetics).

In other words, if we call "affective" that particular class of organic tendencies which appear subjectively in man as "desires" or "appetites" or "needs" and objectively in both man and animals as "movements" completed or incipient (except those that have become mechanical in character), then a large number of the principal "affective tendencies" thus defined may be at once reduced to the single fundamental tendency of each organism to preserve its "physiological invariability."

For instance, we see that hunger, the most fundamental of all affective tendencies, is in reality nothing but the tendency to keep, or restore that qualitative and quantitative condition of the nutritive system of the body which will make possible a continuation of the stationary

[1]Translated for *The Monist* (July, 1911) by L. G. Robinson from *Rivista di Scienza* Vol. XI, 3, 1909.

metabolic state. This tendency of an organism toward the invariability of its own metabolism has become, in the course of its phyletic evolution, an inherent tendency to pass through all the transient physiological states that could re-establish this necessary condition within it, hence, a tendency to perform all movements that have nourishment for their object; yet in doing this it has never relinquished its original character. This results directly from the fact that all inclination to procure new food ceases as soon as the internal nutritive system of the animal has attained its normal state.

Accordingly, the hydra or sea anemone does not react positively to food except when its metabolism is in a state requiring more nutriment, "unless," says Jennings, "metabolism is in such a state as to require more material"; for instance, when the large sea anemone *Stoichactis helianthus* is not hungry, a bit of food placed upon its oral disk occasions the same characteristic "rejecting reaction" as if it were any other disturbing object. And all other organisms, the higher as well as the lower, behave in exactly the same fashion.[2]

Schiff's experiments of injecting nutritive substances into the veins of dogs are direct evidence, on the other hand, that the fundamental condition of hunger is the absence of histogenetic substances in the blood, for these injections resulted not only in nourishing the animal but also in allaying its hunger.

Moreover the fact that hunger, especially as long as it is only moderate, assumes in man the form of a special and localized sensation originating in the wall of the stomach and being the sole cause of the activities

[2]H. S. Jennings, *Behavior of Lower Organisms*, pp. 202, 205, etc. New York, MacMillan, 1906.

induced by real hunger, is—it is scarcely necessary to state—a natural consequence and of but secondary importance. It is only one of many forms in which we see the *substitution of the part for the whole,* and this phenomenon characteristic of all mnemonic physiological processes appears also in the tendency to physiological invariability, which is also essentially mnemonic as we shall see more clearly later on. These peculiar sensations localized in the gastric mucous membrane and produced by its swelling or by some other more or less similar change caused by the empty condition of the stomach, usually take place before or simultaneously with the actual lack of histogenetic substance in the blood, and so finally became representative or vicarious signs of hunger.

The same is true of thirst and of its localization in the upper part of the alimentary canal.

We might pass on from hunger and thirst to the other more or less fundamental organic "appetites" or "needs." All would show us in their different manifestations that they are directed simply and solely toward the restoration of the stationary physiological state, which has been lost or in some way disturbed.

Thus there exists for every animal species an *optimum* of environment with reference to the degree of saturation of the solution in which the animal lives, to the temperature or to the intensity of light, etc., above and below which the organism cannot maintain its normal physiological state and which the animal makes every effort to maintain.

So for instance we see that the infusorian *Paramaecium* at 28° C. reacts negatively toward a rising but not toward a falling temperature, whereas at 22° C. it

reacts negatively toward a falling but not toward a rising temperature. We see also that *Euglena* in a moderate light reacts negatively toward a decrease but not toward an increase in the intensity of light, whereas in a stronger light the reaction is exactly reversed.[3]

The tendency of organisms to maintain their physiological state unaltered consequently resolves itself into a tendency to invariability in their external and internal environments. Thus for instance, oysters and actinians close when exposed to the air; that is, they behave so as to keep the standard of moisture unaltered within themselves and in their immediate surroundings.[4]

To the tendency toward invariability of environment is due also the position which the organism takes with relation to the direction of the various forces to which it is exposed, especially gravity. Hence the tendency to preserve or restore its normal position. Thus, for instance, the amœba draws in its pseudopodia when they come in contact with solid non-edible bodies; but if it is lifted off the bottom of the aquarium and is suspended in the water it stretches out its pseudopodia in all directions. As soon as one of these touches a solid object, the amœba takes hold of it, draws its body over to it, and again resumes its original position. Likewise a starfish when inverted tries to turn over, that is, to return to its normal environmental conditions with relation to gravity.[5]

All "needs" to throw off substances which have been produced by the general metabolism and which the or-

[3]Jennings, *Behavior of Lower Organisms*, pp. 294-295.

[4]H. Piéron, *L'évolution de la mémoire*, pp. 29, 74. Paris, Flammarion, 1910.

[5]K. C. Schneider, *Vorlesungen über Tierpsychologie*, pp. 5, 57. Leipsic, Engelmann, 1909.

ganism can no longer use, are likewise no exceptions to this general rule. For, although the need for eliminating them may be called forth by certain vicarious local sensations capable of evoking the act of expulsion in advance, yet in reality, whether in the case of the smallest and simplest infusorians or of the most highly developed vertebrates, it is due only to the circumstance that the accumulation of this waste material within the organism would eventually disturb its normal physiological state.

To this class of eliminative affective tendencies the sexual hunger seems to belong. For we know that certain recent theories are inclined to regard the whole organism rather than any one definite part of the body as the seat of sexual hunger just as in the case of hunger proper, and at the same time to regard it as due to the need of eliminating the germinal substance.[6]

It may be that just as infusoria after a certain number of divisions become subject to "senescence" (Maupas) so also the germinal substance constantly produced in the adult organism, especially after it has undergone the reducing divisions, may be subject to a similar degeneration if it has not also experienced the requisite caryogamic rejuvenation. Therefore it seems quite plausible that "sexual hunger" is originally nothing but the tendency of the organism to free itself of this "senile corruption" which the germinal substance, being in its nature a nuclear substance awaiting fertilization, produces by means of its hormonic secretions or substances of disintegration and spreads throughout the entire organism.

[6]See, for instance, though only in certain respects, J. Roux, *L'instinct d'amour,* ch. I, "Base organique de l'instinct sexuel." Paris, Baillière, 1904.

The more or less brilliant or striking "wedding garment" which nearly all animals assume when in love, arises from an abnormal condition of general hypersecretion occasioned again by the hormonic products of the germinal substance. At any rate it shows how deep is the physiological disturbance caused in all somatic cells by the germinal substance. The effort to expel so disturbing an element then becomes a tendency to copulation as means of effecting this expulsion. Hence the fundamentally selfish character (*nature foncièrement égoïste*) of sexual love which Ribot rightly emphasizes: "In the immense majority of animals, and frequently in man, the sexual instinct is not accompanied by any tender emotion. The act once accomplished, there is separation and forgetting." [7]

It remains to be explained why copulation of the sexes is the only means of eliminating the germinal substance, whereas the single individual is sufficient for the removal of all other more or less similar waste matter.

It is easy to suppose that the reason lies in the peculiar nature of the substance itself, and there are two circumstances that may perhaps, if considered together, contribute a little to the desired explanation: First, the attraction by the ovum of the spermatozoon even at some distance by means of secretions diffused in all directions; and second, the fact that hermaphroditism probably preceded sexual dimorphism in the phylogeny of pluricellular organisms. Still we must recognize the fact that the phylogenetic process, which by this elimina-

[7] Th. Ribot, *La psychologie des sentiments*, p. 258. Paris, Alcan, 1908 (English translation in Contemporary Science Series, London, 1911, p. 253).—*Essai sur les passions*, pp. 67 ff. Paris, Alcan, 1907.

tion has become so closely associated with copulation, is still far from a satisfactory explanation.

But even in this incomplete form the hypothesis which attributes to the sexual instinct no further significance than a tendency to eliminate a disturbing element, permits us to present this instinct in very different light from that in which it has hitherto appeared. For were this hypothesis to be accepted, the sexual instinct would not have originated and developed for the "good" of the species, but of the individual. It would therefore not represent the "will of the species" imposing itself upon the individual, as most people now maintain with Schopenhauer, but much rather would it mean here as always the "will" of the single individual; that is, the usual tendency to keep its stationary physiological condition unchanged. And instead of seeing in it with Weismann and all neo-Darwinists a new evidence of the alleged omnipotence of natural selection, Lamarck's principle of individual adaptation combined with the inheritance of acquired characters would be sufficient to account for this as well as for all other instincts.

Moreover, the "elimination" hypothesis is sufficient by itself to explain certain peculiarities of this impulse which would be quite incomprehensible from the standpoint of Schopenhauer and the neo-Darwinians.

Ribot, for instance, is surprised that an instinct which is so exceedingly important for the continuance of the species is so often subjected to certain perversions which seem to involve its complete negation.[8]

The fact that such perversions are common accords poorly with the hypothesis that the only reason for the

[8]Ribot, *La psych, des Sent.*, pp. 263, 265 (Engl. ed., pp. 257, 259).

existence of such an instinct is the need for the continuance of the race.

Finally, the fact that both animals and man now desire copulation or even certain secondary sexual relations for their own sakes—hence independently of the act of the elimination of the germinal substance, perhaps even in default of any to eliminate,—this also, as we shall better appreciate later on, is only the consequence of the mnemonic law already mentioned of the substitution of the part for the whole, and of its derivative, the law of the transference of affective tendencies. According to this law all phenomena that constantly accompany the satisfaction of certain affectivities become also in their turn objects of desire, and all habits acquired for the satisfaction or in the satisfaction of certain affectivities likewise become affective tendencies.

If the sexual instinct also, on account of its origin, can be referred to the class of tendencies which serve to maintain the stationary physiological condition of the organism, then the above law is open to no exception as far as the fundamental organic tendencies are concerned. Hence we can sum it up in the following words:

Every organism is a physiological system in a stationary condition and tends to preserve this condition or to restore it as soon as it is disturbed by any variation occurring within or without the organism. This property constitutes the foundation and essence of all "needs," of all "desires," of all the most important organic "appetites." All movements of approach or withdrawal, of attack of fight, of taking or rejecting, which animals make are only so many direct or indirect consequences of this perfectly general tendency

of every stationary physiological condition to remain constant. We shall soon see that this tendency in its turn is only the direct result of the mnemonic faculty characteristic of all living matter.

This single physiological tendency of a general kind, accordingly, is sufficient to give rise to a large number of the most diversified particular affective tendencies. Thus every cause of disturbance will produce a corresponding tendency to repulsion with special characteristics determined by the kind of disturbance, by its strength, and by the modes of reaction tending to circumvent the disturbing factor; and for every incidental means of preserving or restoring the normal physiological condition, there will be a quite definite corresponding tendency such as "longing," "desire," "attraction" and so forth.

Even the instinct of self-preservation—when understood in the usual narrow sense of "preservation of one's own life"—is only a particular derivative and direct consequence of this very general tendency to preserve physiological invariability. For every condition which would eventually lead to death first presents itself as a mere disturbance, and it is only as such that the animal tries and learns to avoid it. Jenning's amœba, for instance, which had been completely swallowed by another amœba, but had succeeded in getting away, did not in all probability flee from a phenomenon that endangered its life, but from a condition in its environment which even though a profound disturbance, was nevertheless nothing but a disturbance.

It is well known that Quinton was the first to develop a theory that organisms tend to maintain in their internal intercellular environment the same chemical

and physical conditions that obtained in the primordial environment when life first appeared on earth.[9]

But it is easily seen that our theory is limited to a consideration of the tendency to invariability only so far as it manifests itself each moment in the behavior of each individual. Therefore instead of serving as a far too one-sided starting point for the explanation of the evolution of species it forms the basis upon which all the most important affective tendencies of the animal world may be built up.

As a factor of invariability for the individual, this tendency to preserve its stationary physiological condition is indeed one of the most important factors in the variation and progress of the species, but in quite a different way from that pointed out by Quinton. For from this tendency arose and developed the power of motion which is the greatest difference between plants and animals, and with which also has kept pace the development and perfection of the whole motor apparatus, including that of the nerves and senses, which plays so important a part in determining the characteristics which distinguish the different zoological species.

Finally as a factor of individual invariability it has proved by its effect on man to be one of the most conspicuous factors in all social evolution, for we may well say that technical inventions and industrial products from the first cave dwellings, the first skins used for clothing, the first discovery of fire to the most complex attainments of to-day have tended constantly more or less directly or indirectly towards one single goal,

[9]R. Quinton, *L'eau de mer, milieu organique.* Especially Book II, "Loi génèrale de constance originelle," pp. 429-456. Paris, Masson, 1904.

namely the artificial maintenance of the greatest possible constancy in the environment, which is the necessary and sufficient condition for preserving physiological invariability.

II.

Closely connected with this inherent fundamental tendency of every organism to strive to preserve its normal physiological condition or to restore it as soon as it is disturbed, is still another attribute which in its turn becomes the source of new affectivities.

For as soon as the previous stationary condition cannot be restored by any means, that is by any movements or change of location, the organism disposes itself in a new stationary condition consistent with its new external and internal environment. In this way there originate a large number of new phenomena called "adaptations."

Thus, for instance, Dallinger's classical experiments on the acclimatization of lower organisms—suggested by the observation that many organisms usually living in water of an ordinary temperature, also live and flourish in the hottest spring,—have proved that Infusoria may gradually become accustomed to a constantly higher temperature so that finally after years of continuous slow increase in the degree of heat, they can stand a temperature so high that any other individual not acclimated would certainly die if subjected to it. It is likewise known that the same species of Protozoa are found in both fresh and salt water, and that it is possible to accustom fresh-water Amœbæ and Infusoria to a salt habitat which would have killed them at the start,—and there are more instances of the same kind.[10]

[10]See C. B. Davenport and W. E. Castle, "On the Acclimatisa-

One feature of special interest to us is the fact that the new conditions of the environment to which the animal gradually becomes accustomed tend in time to become his *optimum*. "This individual adaptation (e. g., to a different proportion of salt) is effected in accordance with the rule that the conditions of density under which an individual is living, tend to become in time the *optimum* conditions for that individual." [11]

This may be observed even in plant organisms. Plasmodia of the Myxomycetes die when plunged suddenly into 1 or 2% glucose solutions, and even draw back from ½ or ¼% solutions, and yet they may gradually become accustomed to 2% solutions so that they finally show by their behavior that they prefer their new environment to the original one without glucose.[12]

The diatom *Navicula brevis* ordinarily shuns even the weakest light and tries to hide itself in the darkest part of the drop of water in which it is being observed. However, if a culture is placed in the bright light of a window for two weeks, it exhibits exactly the opposite tendency and makes for the brightest part of the drop as soon as it is removed again to its former position in a weak light.[13]

The common actinian (*Actinia equina*) often found clinging to rocks in all possible positions with relation to the force of gravity, sometimes with the axis of the

tion of Organisms to High Temperatures."—*Archives für. Entw.-Mech. der Organismen*, II, 2. Heft, July, 1895.—C. B. Davenport and R. V. Neal, "On the Acclimatisation of Organisms to Poisonous Chemical Substances," *loc. cit.*, II, 4. Heft, Jan. 1896.

[11]Davenport and Castle, *op. cit.*, p. 241.

[12]E. Stahl, "Zur Biologie der Myxomyceten," *Bot. Zeit.*, Mar. 7, 14 and 21, 1884, p. 166.

[13]Davenport and Castle, *op cit.*, p. 246.

body directed upward, sometimes downward and sometimes to one side, seems to become so accustomed to its position that it tries to assume the same one when removed to another spot. For instance, if several actinians found in various positions are collected and placed in an aquarium, "they show in attaching themselves a distinct tendency to assume the same position they had formerly adopted." [14]

We might bring forward innumerable other examples but are here chiefly concerned with pointing out their significance. They show that the new physiological state arising from adaptation to the new environment, when once it has supervened and has existed a certain time within the organism, tends thereafter to preserve or restore itself. This tendency of a past physiological state to remanifest or reproduce itself is nothing but the tendency inherent in every mnemonic accumulation to "evoke" itself again. Hence it is a tendency of a purely mnemonic nature.

From this then it follows directly that the tendency to physiological invariability from which originate, as we have seen, the most important organic affective tendencies of all organisms must be equally mnemonic in nature. For if according to the above mentioned examples an entirely new and recent physiological state is nevertheless able to leave behind a mnemonic accumulation producing a distinct tendency to its own restoration, it is easy to understand that in proportion as the normal physiological state persists longer it must possess a correspondingly stronger mnemonic tendency toward its restoration whenever it is disturbed.

This then implies that each of the innumerable

[14]Piéron, *op cit.*, p. 144.

different elementary physiological states, of which each is effective at one definite point of the organism, and all combined constitute the general physiological state, possesses the faculty of depositing independently a "specific accumulation," from all indications similar to that deposited in the brain by each of the nervous currents which make up the different sensations and leave behind a mnemonic residue capable of being reactivated or revived, By "specific accumulations" of the various nervous currents we mean here only that every accumulation is capable of giving as discharge only that particular specificity of the nervous current by which this accumulation has itself been deposited.

The extension of this faculty of "specific accumulation" to all physiological phenomena in general accords with the hypothesis that nervous energy is the basis for all the phenomena of life. If in the psychomnemonic phenomena properly so called the action of nervous energy produced by "discharge" or by stimulation of the respective center appears in the foreground, whereas the specific physico-chemical phenomena accompanying the discharge remain in the background so that until recently they were quite overlooked, that would be—according to the fundamental concept of Claude Bernard on the essential identity of all the different forms of irritability of living matter—a difference of degree only but not of essence, inasmuch as true physiological phenomena accompanying the respective stimulation (muscular contraction, glandular secretion, etc.) appear with greater distinctness, whereas the specific nervous phenomena which likewise accompany this physiological activity are less perceptible. In this way we have tried to explain the fundamental mne-

monic property of all living substance which has recently been especially emphasized by Hering, Semon and Francis Darwin, and also to explain the most essential and significant biological phenomena proceeding from it either directly or indirectly.[15]

By this extension of the mnemonic faculty to all elementary physiological phenomena we now obtain a somatic or visceral theory of the fundamental affective tendencies in the sense that the tendency toward physiological invariability or toward the restoration of this or that previous physiological state corresponding to this or that previous environment, depends on innumerable elementary specific accumulations, differing from point to point of the body and whose combined potential energy would form as it were a "force of gravitation" toward that environment or those conditions which make possible the preservation or restoration of the combined physiological system represented by all these elementary accumulations.

Naturally in organisms supplied with nervous systems there would arise and be gradually developed side by side, in cooperation with, and often as a substitute for, every one of these affective tendencies of purely somatic origin and seat, the affective tendency represented by the corresponding mnemonic accumulations which had been deposited in that particular zone of the nervous system directly connected with the respective points of the body. In man, for instance, this zone

[15]See above the chapter on "The Phenomena of Memory and the Vital Phenomena." See also "Die Zentroepigenese und die nervöse Natur der Lebenserscheinung," *Zeitschr. f. d. Ausbau d. Entwicklungs-lehre*, II, 1909, Heft 8-9—"Das biologische Gedächtnis in der Energetik," *Annalen der Naturphilosophie*, VIII, and *Scientia*, XI, 3, 1909.

would be Flechsig's *Körperfühlsphäre* to which in certain cases may also be added the frontal zone.[16]

Now after the cerebral mnemonic accumulations had arisen phylogenetically under direct somatic action, they would finally have become able to represent by themselves, even if all connection with the body had been severed, those former affective tendencies to which they owed their origin. And indeed this is true because of the two fundamental mnemonic laws of (1) the gradually increasing independence of the part with reference to the whole and (2) the substitution of the part for the whole, which arise directly from the fact that every elementary specific accumulation when once deposited is capable of an independent existence. Therefore Sherrington's "spinal" dog, for instance, continued to experience the same repugnance to the flesh of other dogs, to exhibit other similar affectivities and even the same emotions as the normal dog, though all of them are undoubtedly of phyletic somatic origin.[17]

But this cooperation and this possibility of an eventual substitution of the affective tendency whose seat is in the brain, for the corresponding affective tendency of somatic origin, does not prevent the former from being entirely in the control of the latter. Therefore modern psychology generally admits that the affective life "has its cause below in the variations of the cenes-

[16]P. Flechsig, *Gehirn und Seele*, pp. 19, 21-22, 92, 99-100. Leipsic, Veit. 1896.

[17]See C. S. Sherrington, *The Integrative Action of the Nervous System*, pp. 260-165. London, Constable, 1906. Cf. the pertinent discussion of these experiments by Lloyd Morgan, *Animal Behaviour*, 2d ed., p. 292, London, Arnold, 1908; and Revault d'Allonnes, *Les inclinations*, pp. 101 ff., Paris, Alcan, 1908.

thesia, which is itself a resultant, a combination of vital operations." [18]

Nor does it in the least prevent affective tendencies from keeping all the fundamental properties which they owe to their mnemonic visceral origin, of which the most important are first the possession of a "diffuse" seat, and second that they are eminently "subjective."

For every stationary physiological system in equilibrium with regard to its environment permeates the whole organism and consequently also all that part of the brain in which this organism is reflected. Accordingly, in contrast to the mnemonic sense-accumulations each of which to all appearances has a seat distinctly localized at a single point or in a single center of the cortex of the brain, we have every reason to conclude that each affective tendency is made up of an infinitely large number of different elementary mnemonic accumulations, deposited respectively in every point of the body and in every corresponding point in the brain.

To this mnemonic physiological origin of the affective tendencies is also due their eminently "subjective" character; for the organism is equipped potentially with this or that "idiosyncratic" affective tendency, with this or that "appetite," according to the various environments or conditions in which the species and the individual were placed for a longer or shorter time in the past, in other words according to their individual history.

Hence the subjectivity and infinite variety manifest in the needs, the appetites and desires and consequently in everything that furnishes an object of "affective evaluation."

[18]Ribot, *Psych. des sent.*, p. 10.

III.

The hypothesis here presented of the mnemonic nature of the affective tendencies in general is further confirmed by other examples of more special affectivities which have also originated by way of "habit" and yet bear special relations to the environment since they affect only one part or another of the organism and manifest an activity only periodically or intermittently. They are especially in evidence in the higher animals and in man most of all.

As a typical instance it will be sufficient to consider maternal love.

Evidently the habit of having certain relations of parasitism, or, in general, of symbiosis, with the progeny throughout a long series of generations has become gradually transformed in a mnemonic way into affective tendencies towards these relations.

"Comparative ethology," says Giard, "shows us most clearly that the relations between the parent organism and its progeny are in principle absolutely the same as those existing between a parasite and the animal it lives upon, and that after a period of unstable equilibrium in which one or other of the two associated organisms suffers to the advantage of its companion there is a tendency to the establishment of a definite position of mutual (*mutualiste*) equilibrium." [19]

This is true for instance of the relations of internal incubation, which though first sought and effected by the embryo itself in some phase of its development for the purpose of nutrition or some other advantage, and

[19] A. Giard, "Les origines de l'amour maternel," *Revue des idées*, April 15, 1905, p. 256.

at first simply endured by one of the parents, either father or mother, finally become actual "needs" to this parent.

It is likewise true of the relations of external incubation (brooding) which arise at first as the result of some particular circumstance and in this way become a habit. For instance the attachment manifested by the female spider *Chiracanthium carnifex* for her nest, whether it be her own or one of which she has taken possession, grows with time, that is with the length of her occupation of it. Hence "mother love" seems in her case to be really nothing but her attachment to a home to which she has become accustomed.[20]

It is just the same with the brooding of birds and some reptiles, which owes its origin to the pleasant sensation which the contact with the fresh eggs brings in the feverish condition accompanying the egg-laying process, but which by habit has become in itself an instinctive inclination.[21]

Finally as regards lactation the young have gradually developed secretions in the lactiferous glands by sucking the secretions of the perspiratory glands on the breast of the mother brooding over them, and thus they have at the same time so accustomed the mother to this process that lactation finally becomes an actual need for her. "With mammals we must look for the origin of the mutually symbiotic relations which unite mother and child in the phenomenon of lactation. The physiological disorders of pregnancy and parturition lead, among other very curious trophic effects, to an excessive secretion of

[20]A. Lécaillon, "Sur la biologie et la psychologie d'une araignée," *Année psychologique,* Année 10e, pp. 63-83. Paris, Nasson, 1904

[21]Giard, *op. cit.,* p. 266.

the mammary glands which, as we know, are only locally specialized sebaceous glands of the skin. The young animal in taking its first nourishment thus alleviates the discomfort of the female and becomes a means toward the comfort of its mother." [22]

That the need for lactation is the origin of maternal love is shown by the fact that the mother who is deprived of her young tries to replace them by foster-nurslings. "The necessity of getting rid of a troublesome secretion is powerful enough sometimes to cause the female that lost her young to steal the progeny of another, and these robberies have been performed even by females that were still suckling their own young, the satisfaction of a need leading them, as is generally the case, to seek a still greater satisfaction which might lead even to excess." [23]

In the cases observed by Lloyd Morgan, this need of the mother takes the form of a mother love solicitous for the nourishment of her young, and it is possible that it may actually represent in them the beginning of an unselfish attachment. "Further, I have seen both bitches and cats get up and again lie down so as to bring the teats into closer proximity to the mouth of any young which failed to find them. It has been noticed by a man who is a remarkably good observer and has had much to do with animals, and also by myself, that when a lamb is weakly and fails to find the teat, the mother not infrequently uses its shoulders, head and neck as a lever to place the lamb on its legs; and, having accomplished this, straddles over the lamb, and brings the teats against

[22]Giard, *op. cit.*, pp. 269-270.
[23]Giard, *loc cit.*, p. 270.

its lips; and these efforts are continued until the little animal sucks." [24]

This example is very significant for it shows clearly how the necessity for the elimination of the milk must end in arousing an attachment for the nursling as the customary means for attaining this end, just as we have seen that the need for the elimination of the germinal substance must lead to an affectivity for the other sex, here again as the customary means to effect this elimination.

Just as "sexual attraction" ceases after the elimination of the germinal substance, so also does "mother love" disappear as soon as the need for lactation is no longer felt. "Maternal affection does not generally survive the causes which produced it and only vague traces of it are noticeable after lactation has ceased." [25]

Finally, the fact that the mother's affection is stronger than that of the father, and that the parents' love for their children is stronger than that of the children for their parents confirms the hypothesis that all these affectivities have arisen exclusively by way of habit, for it shows that affection for those with whom we have certain relations is the more intense the more numerous and prolonged these relations are. "Among animals as a whole," remarks Ribot, "paternal love is rare and inconstant and among the lower representatives of mankind it is a feeble sentiment and forms but a slight bond." [26] Paternal love exists only where the union of the sexes is close, that is, where the communal life

[24]Lloyd Morgan, *Habit and Instinct,* p. 115, New York, Arnold, 1896.

[25]Giard, *op. cit.,* p. 273.

[26]Ribot, *psych. des sent.,* 285.

"creates a current of affection because of services rendered." [27]

"Every one recognizes," says Pillon in his turn, "that the love of parents for their children exceeds in intensity the children's love for the parents, and that of the two parents it is the mother whose love is stronger for her child. . . . The reason is that in the mother's case much more than with the father the love for the child is nourished and stimulated, because of her special functions, that is, by the constant performance of the actions it dictates." [28]

But mother-love and mutual love within the family in general, owing its origin to certain relations grown into habit, represents only one particular case of a universal law. For every other relation to person or things (no matter how special) which becomes in the slightest degree a habit finally appears for this very reason as something "desired." In every environmental relation whether general or particular is verified Lehmann's law of the "indispensability of the customary," which this investigator established for every stimulus to which one becomes accustomed and whose cessation arouses a need for its presence.[29]

"I have a small clock in my room," a friend once wrote to G. E. Müller, "which will not run quite twenty-four hours with one winding. It often happens therefore that it stops. Whenever this occurs I notice it at once, whereas of course I do not hear it at all when it is

[27]Ribot, *Psych. des sent.*, p. 286.

[28]F. Pillon, "Sur la mémoire et l'imagination affective," Année *philosophique*, XVII, 1903, pp. 69-70. Paris, Alcan, 1907.

[29]A. Lehmann, *Die Hauptgesetze des menschlichen Gefühlslebens*, pp. 194 ff. Leipsic, Reisland, 1892.

running. The first time this occurred the sensation was somewhat as follows: it happened that I was suddenly aware of a very indefinite unrest, a lack of something without being able to say just what the matter was. Not until after some reflection did I discover the cause in the stopping of my clock." [30]

Moreover each of us has doubtless had opportunity to observe how things which are disagreeable at first finally become attractive from custom, and how such habits assumed in the course of man's life become as peremptory "needs" as those which we call natural needs. "Smokers, snuff-takers, and those who chew tobacco, furnish familiar instances of the way in which long persistence in a sensation not originally pleasurable, makes it pleasurable—the sensation itself remaining unchanged. The like happens with various foods and drinks, which, at first distasteful, are afterwards greatly relished if frequently taken." [31]

Thence arises the hankering after certain customary things which we suddenly miss: "In some animals there is produced a condition resembling nostalgia, expressing itself in a violent desire to return to former haunts, or in a pining away resulting from the absence of accustomed persons and things." [32]

Mere habit, therefore, is enough, as we have seen in the case of family love, to cause other similar affectivities also to originate and take root. Such are gregariousness, sociability, friendship, and the like: "The perception of

[30]G. E. Müller, *Zur Theorie der Sinnlichen Aufmerksamkeit*, p. 128, Leipsic, Edelmann.

[31]Herbert Spencer, *The Principles of Psychology*, 4th ed., I, 287. London, Williams and Norgate, 1899.

[32]Th. Ribot, *Essay on the Creative Imagination*, p. 95. Chicago, The Open Court Publishing Company, 1906.

kindred beings, perpetually seen, heard, and smelt, will come to form a predominant part of consciousness—so predominant a part that absence of it will inevitably cause discomfort." [33]

Finally we are all well aware of the powerful influence of the habits of life current in any family circle during the earliest years of a child's life—"nurture" in its broad sense, as Galton would say—because from these habits arise and grow the feelings and moral tendencies which remain impressed upon the whole life as though they were "innate." [34]

In short from these few instances adduced simply in explanation of our position, we see how profound is the truth contained in the saying that habit is a "second nature."

But if to a certain extent we can see the most diverse tendencies originate by way of habit before our very eyes, then we may also attribute a similar mnemonic origin to all affective tendencies, since the nature of innate tendencies differs in no wise from that of acquired tendencies. Very similarly in the case of morphological evolution we may consider that the Lamarckians are quite justified in drawing from the few observable cases of adaptation acquired during life, the conclusion that the entire structure of the organism owes its existence to an infinite number of similar functional adaptations.

Hence we may complete the saying quoted above with the phrase that on the other hand "nature" is nothing but a "former habit."

[33]Spencer, *op. cit.*, II, 626.

[34]Francis Galton, *Inquiries into Human Faculty and Its Development*, pp. 208-216. London, MacMillan, 1883.

IV.

The hypothesis of the mnemonic origin and nature of all affective tendencies finds still further support in a property which is inherent in all of them, namely their "transference" which likewise is itself essentially mnemonic and by which all other affectivities are derived from those of direct mnemonic origin and thus come to have an indirect mnemonic origin (Ribot's "law of transference").

For in consequence of the "substitution of a part for the whole," a fundamental mnemonic principle frequently mentioned above, it happens that merely parts or fragments of certain environmental relations, striven for originally in their totality, or that "analogous" environmental relations, i. e., those that are only partly similar to one desired, or that environmental relations constituting "means" suited to the attainment of an "end" and therefore its necessary precursors, or, in fine, that environmental relations which constantly accompany this "end," evoke the same affectivity as the original "end" itself. Hence this affectivity is "transferred" from the whole to the part, and this attachment for the part then becomes so much stronger that this partial relation which is first sought as a substitute for the whole finally constitutes in its turn an habitual environmental relation henceforward desired or sought for its own sake quite apart from the real and original affective "transference."

This is the case for instance, as has been mentioned above, with regard to copulation, the customary means for the elimination of germinal substance, and also with regard to the secondary sexual relations as phenomena usually accompanying copulation. The "conquest" of

the other sex though only a necessary means for the satisfaction of sexual appetite finally becomes with certain individuals an end in itself. The pleasure in seducing for its own sake, the "sexual vanity" of both male and female and the other similar affectivities are further instances.

The case is the same with the tearing to pieces of prey which was originally the customary means for satisfying hunger but finally gave place to cruelty for cruelty's sake.

"One half of the animal race live upon prey; and as it is delightful to eat so it must be delightful to kill. Pleasurable also must be all the signs of discomfiture, the helpless struggles and agonized gestures of the victim." [35]

In man the love of victory for its own sake, ambition, thirst for power, desire for fame and glory, the endeavor to surpass his fellows, are all derived as consequences of further transference.

In these and all other similar cases of affective transferences to environmental relations constantly becoming less material and more moral, besides the real proper affective transference which transforms the part into a new "end," there is always involved in man and in the higher animals the cooperation of their own intellectual development.

For the intellect is constantly discovering new and unsuspected similarities between the most diverse phenomena, even between material and ethical phenomena, extending the same affectivities to the one class that are valid for the other; just as disgust for certain foods characterized by taste or odor as unwholesome extends

[35] Alexander Bain, *The Emotions of the Will*, 4th ed., London, Longmans Green, 1899, p. 65.

to certain objects which can only be touched or seen (viscous bodies), and then, carrying the analogy still farther, even to simple "objects" or relations of an ethical order.[36]

At the same time inasmuch as the intellect foresees with constantly increasing sharpness the external phenomena to be expected as effects of given causes, it continues to devise new means more indirect and more complex for attaining its end, and thereby to open a broader sphere of efficiency for "affective transference." For instance the weapon which was invented by man as means for self-preservation has rendered possible an affective transference to itself which is characteristic of the warrior and the hunter; and the earth which the agriculturist has utilized to provide his own nourishment has made possible that intense love for the soil frequent among farmers.

Furthermore, since the intellect also foresees with increasing certainty internal physical processes, it calls into being a large number of new affectivities destined to prevent possible future affective tendencies from remaining unsatisfied. For instance the anticipation of future hunger gives even the satiated man the inclination to lay up food that is left from a meal, and to keep it in his possession. Thus arises in general the sense of ownership, and in the same way the anticipation of the innumerable other desires which civilized man cherishes today excites in him an intense longing for wealth, covetousness and similar passions.[37]

Finally, the intellect renders possible that infinite vari-

[36]Ribot, *Psych. des sent.*, p. 212.—*Essai sur les passions*, pp. 65 ff.

[37]Spencer, *Princ. of Psychol.*, I, 488 f.—Ribot, *Psychol. des sent.*, 110, 269-270.

ety of shades of which affective tendencies are capable in man. For since it is able to observe from different points of view, simultaneously or nearly so, all environmental relations even when only slightly associated, it can evoke diverse affectivities at the same time, and these, as Bain would say, by association, combination, confluence, interference or mutual partial inhibition, finally produce an exceedingly complex affectivity which is therefore capable of showing the finest imaginable gradations from one case to another according to the number and character of its component parts.

Thus, for instance, fear, anxiety and kindred feelings had already developed in animals from the instinct of self-preservation in its purely defensive form; but in man this latter gave rise also to all the propitiatory affectivities in innumerable varieties and shades, such as prostration, humility, hypocrisy, flattery and the like. Even the religious sentiment in its lowest forms is a direct consequence of this propitiatory affectivity, while the loftier religious sentiment and the kindred feeling experienced in the presence of the sublime are more highly developed and more complete forms of the same thing.[38]

Similarly from the instinct of self-preservation in its double aspect, offensive and defensive at the same time, had already developed in the higher animals the instinct to attack and all the different varieties of counter-attack; but in man this instinct has assumed the most varied forms and shades from deepest hatred to a scarcely perceptible antipathy, from rapacity to the merest envy, and from the most violent thirst for revenge to the slightest resentment. The noble sentiment of justice is a very

[38]For instance, see Ribot, *Psych. des sent,* p. 100, and E. Rignano, "Il fenomeno religioso," *Scientia,* XIII, 1, 1910.

remote and hardly distinguishable derivative of the same instinct.[39]

How high may be the degree of complexity which can thus be attained is attested, for instance, by maternal love which has grown from the purely bodily necessity for lactation to the tenderest feelings of the noblest self-denial, and especially also by conjugal affection which has been transformed from coarse brutal sexual appetite to an harmonious cooperation of the gentlest and most delicate moral affectivities.[40]

Yet it is easily comprehensible that it would be useless, and impossible to stop here to investigate all of the affectivities and their slightest shades which have arisen and in this way attained their development in the higher animals and especially in man. Let these few indications suffice to render intelligible the fact that as soon as the organism has acquired in the direct mnemonic way a stock of affective tendencies and the intellect has attained its proper development, the number of affectivities which may be derived by "transference" and by "combination," that is to say, by indirect mnemonic means, is infinite.

V.

But few words are needed to indicate the place of affective tendencies among those fundamental physical phenomena which are most closely connected with them, such as the emotions, the will, and the states of pleasure and pain.

Emotions are only sudden and violent modes of acti-

[39]See Bain, *The Emotions and the Will,* pp. 117 f.—Ribot, *Psych. des sentiments,* pp. 229 f., 271 f.—*Problèmes de psychologie affective,* chap. III, "L'antipathie," Paris, Alcan, 1910.

[40]Spencer, *op cit.,* I, 487 f.

vation of those very accumulations of energy of which the affective tendencies consist.

Of course it is not always possible clearly to distinguish affective tendencies from emotions since the former are perceptible neither objectively nor subjectively as long as they remain in a potential state, but become so at their activation which, when sudden and violent, represents the corresponding emotion. But the importance and necessity of distinguishing accurately between emotions and affective tendencies—a distinction however which is usually entirely neglected by most psychologists—lies in the fact that one and the same affective tendency may according to external circumstances give rise to the most diverse emotions, to the most diverse degrees of their intensity, or even to no emotion at all properly so called. For instance if we see a vehicle approaching at a distance we quietly step aside out of the way, but if it appears suddenly before us at an abrupt turn in the street we feel a strong emotional shock. And the same affective tendency of the dog towards a piece of meat can give rise to flight, anger, or the careful, coolly calculated search for a safe hiding place, according to the circumstances under which his dainty meal is endangered.

In short, every emotion, as Stout rightly emphasizes, presupposes an affective tendency, but the reverse does not follow; for an affective tendency even when in full activation need not always imply any emotion.[41]

Every affective tendency "impels" to action, that is, it not only "starts" but really "impinges" upon the organs of motion either directly as in the lower organisms or by the aid of the nervous system as in the higher.

[41]See G. F. Stout, *A Manual of Psychology*, 2d. ed., p. 305, London, 1907.

Therefore from the first moment of its activation it has the appearance of a "movement in the nascent state" (Ribot).

If its activation is sudden and intense the resulting activity of the motor muscles is accompanied by that of all the viscera. This "visceral cooperation" which thus takes place in connection with the emotions properly so called, is not, as Sherrington believes, due solely to the fact that the rapidity and intensity with which the muscles are set in motion induces the immediate action of the viscera which furnish the muscles wth the material for their energy, but also and especially because there is an overflow of nervous energy, which suddenly released in great quantities acts like a flood, and pours forth in numerous other tracks than those closely connected with the locomotor apparatus.[42]

And this visceral commotion thus produced as a result of the sudden intense impulse, according to the well-known theory of James, Lange and Sergi, finds its centripetal echo in the brain in the form of an emotion.[43]

Hence it is the affective tendency which impels us and not the emotion as Sherrington maintains in accordance with the prevalent confusion between affective tendency and emotion which cannot be too greatly deplored, and the emotion is only the reaction of a too rapid and intense manifestation of this tendency.

On the other hand if on account of external conditions or the psychic disposition of the individual the activation of the affective tendency takes place neither too

[42]See Sherrington, *The Integrative Action of the Nervous System,* pp. 265 f.

[43]See the famous article of W. James, "What is an Emotion?" *Mind,* April, 1884. pp. 188-205.—Revault d'Allonnes, *Les inclinations,* 108 f.

suddenly nor with too great intensity, then only are the requisite muscles called into play without any emotion. Thus the amount of useful work accomplished as a result of the discharge of the affective tendency is greater in inverse proportion to the amount lost in the coordinated movements of a purely emotional significance. This is the reason why we generally observe the greatest determination, the most tenacious persistence in transactions, the most intense and feverish activity in "unemotional" individuals.[44]

As regards the will, an act of volition takes place whenever an affective tendency directed towards a future goal triumphs over an affective tendency whose aim is for the present; in other words, whenever a far-sighted affectivity is victorious over a short-sighted one. It is not the man who sweating and panting after a long run throws himself down to drink eagerly from a spring who exercises an act of volition, but rather the one who forbears to slake his burning thirst for fear of a greater future evil. Likewise no act of volition is exerted when an exhausted wanderer throws himself down to sleep, but rather when a mountain climber overcomes exhaustion in order to reach the desired goal. And the act of a man who on a momentary impulse falls upon his opponent at the slightest provocation with hard words and fisticuffs does not demand any will power, as does the conduct of the man who bridles his just anger in order coolly to estimate to its remotest consequences the most appropriate procedure to enter upon against the offender.[45]

[44]See Revault d'Allonnes, *Les inclinations*, pp. 207 f.

[45]Cf. E. Meumann, *Intelligenz and Wille*, pp. 181 f. (Leipsic, Quelle und Meyer, 1908), although differing in many points.

Essentially then the will is nothing else than a true and proper affective tendency which checks other affective tendencies because it is more far-sighted and which in its turn impels to action like all affective tendencies. "There is present in the action of will some desire of a good to be obtained or of an evil to be shunned, which imparts its driving force." [46]

Two extreme instances deserve special mention, for they include all other cases. The first of these may again be divided into two.

Sometimes one of the affective tendencies is so strong and persistent that it constantly outweighs all others; it checks them if it is contrary to them and strengthens them if it is in harmony with them. Such an "hypertrophied" affective tendency is called "passion" (Ribot, Renda). If it is directed towards some present aim we say that it overthrows the will because it successfully withstands the inhibitive effect of every other affective tendency directed towards the future; if on the other hand its own aim is in the future, an "ideal" whose attainment may require the work of a lifetime, then we say that the individual is persevering, stubborn, unyielding, endowed with an iron will, because every other opposed affective tendency directed toward an immediate end dashes in vain against it.

On the other hand it sometimes happens that the two conflicting affective tendencies are evenly balanced. At one moment the far-sighted tendency gains greater force and seems to triumph by turning the mind to new consequences in the future, but the next instant the short-sighted tendency discovers new or more clearly recog-

[46]Maudsley, *The Physiology of Mind*, p. 339. London, MacMillan, 1876.

nized aspects in the object desired for the time being, and becomes more intense, threatening again to gain the upper hand. The individual then falls in a state we call "indecision." When a philosopher discovers by introspection that he is in this situation, he will easily realize that both affectivities exist together within him, that they are "flesh of his flesh," and that the slightest and most insignificant physical occurrence is enough to cause either one to gain ascendency over the other. It is clear that he can easily fall a prey to the illusion that nothing at all, any chance breath of wind, is enough to give one the preponderance over the other. This is the subjective illusion of free will which for many centuries has constituted the greatest and most difficult problem that philosophy has been called upon to solve.

Finally to come to the consideration of "pleasure" and "pain," it is the merit of the modern psychological school that it has shown the fallacy of Bain's theory that the fundamental fact of animal life is the pursuit of "pleasure," in other words, the search for everything pleasant and the avoidance of everything unpleasant; and on the other hand that it has clearly emphasized that the conditions of pleasure and pain represent only the superficial part of the affective life, "of which the deep element consists in affective tendencies, positive or negative. . . . These are the elementary processes of affective life, of which pleasure and pain represent only the satisfaction or failure." [47]

Since an activation of nervous energy accompanies every "satisfaction" of any affective tendency, and every "disappointment" corresponds to an interruption or cessation of this energy, pleasure really corresponds to every

[47]Ribot, *Psychol. des sent.*, p. 2.—*Probl. de psych. aff.*, p. 16.

state of discharge or activation of the nervous or vital energy, and pain to every state of inhibition or suppression of it.

In fact "painful" is every act inhibitive of certain nervous activities; "unpleasant" every too perceptible change of surrounding conditions which renders impossible the continuance of the hitherto stationary physiological state, "agonizing" every sudden and violent change of environment which brings about the complete stoppage or destruction of life in one or another part of the organism, and "sad" is the individual when there is a general diminution of vital functions within his organism.

Inversely, it is "pleasant" to exercise one's muscle in play and sport; the cessation of a strained condition of the soul is a "relief," the return to an accustomed environment and the resumption of habits is "welcome," and in general full of "joy" and "pleasure" is every state in which the organism experiences a greater activity of nervous energy.[48]

It is sufficient here to indicate that the theory of the mnemonic origin of all affective tendencies which we have endeavored to explain and substantiate in this essay, offers a new argument in support of the modern psychological views with regard to the inmost nature of pleasure and pain. For in assigning to these affective tendencies the nature of mnemonic accumulations it implies that the fundamental principle of affective life can be nothing but the tendency to activation inherent in these accumu-

[48]See Ribot, *Psych. des sent.*, Part I, chapters I-III, especially pp. 52 f. and 83 f.—W. Ostwald, *Vorlesungen über Naturphilosophie*, pp. 388 ff. Leipsic, Veit. 1905

lations, such as exists also in every other accumulation of potential energy, and that therefore pain and pleasure, pleasant and painful states, can be nothing but the superficial and subjective side of this activation or of its inhibition.

VI.

Before terminating these few notes upon the nature of affective tendencies, we shall add a few remarks, which seem to us indispensable, on the fundamental character of these tendencies, according to which they constitute a force, so to speak, with a definite end to be attained but with the path to be followed left undetermined.

Affective tendencies owe this property of gravitating toward an end while the means remain undecided, to the circumstance that they depend on the existence in a potential state of a certain general or local physiological system or state, which was determined in the past by the outside world as a whole or by individual particular relations to this outside world, and which now like every other potential energy simply endeavors to reactivate itself as soon as it is released by the persistence or recurrence of even a small part of this environment or these environmental relations. For the result of the existence of this tendency is that the organism gravitates toward this environment or these environmental relations rendering possible the recurrence of this physiological state, but it does not imply any "impulse" toward or "impingement" upon any one of the series of passing physiological states or movements which, even if they were capable of eventually bringing the organism back to the desired environment, nevertheless have nothing in common with

the definitive physiological state itself which corresponds to this environment.

Only from the moment when one series of movements happens to bring the organism back to the desired environmental relations earlier than another one, will it have acquired an advantage over the others, and this result may be expressed by saying that the affective tendency has exercised a "choice" (James, Baldwin and the American school in general).

Hence it is only from that moment that the affective tendency will by mnemonic association constitute a force which "impels" these movements toward the end, just as certain reflex movements "impinge" on one another (Sherrington). And only from that moment will these movements (so long as they have not become mechanical in the form of reflexes) be determined exclusively under the pressure of the corresponding affectivity or the equivalent "act of the will."

However, until this takes place the affectivity betrays no tendency at all to discharge in one path rather than in another, hence the great difference between the affective tendency or act or will on the one hand, and the reflex movement on the other. This reflex movement, by means of which the act so "chosen" when often repeated becomes by mnemonic accumulation gradually mechanical and quite independent of the whole, represents a tendency to discharge along one single given path which is determined in advance. It is a force whose point of application and direction are known beforehand, and might therefore be indicated graphically by the customary arrow used to represent the forces of mechanics. On the other hand the affective tendency constitutes a force of which neither the point of application nor the direction

are predetermined but only the point towards which it tends. It is a "disposable" energy to be applied at will to this or that act so long as it leads to the desired end. Therefore it can be represented at the same time quite indefinitely by any of the infinite number of arrows which fill the entire volume of a cone and converge at its apex.

The reflex movement admits therefore of but a single solution. On the other hand the affective tendency admits of an indefinitely large number of solutions so long as none of the possible movements has been performed by chance and given rise to a choice; or when there are numerous equivalent paths to the goal.

This possibility of many solutions constitutes exactly the "unforeseen," the "antimechanical" behavior dependent on the affectivity or will, in contrast to the predetermined mechanical behavior of reflex movements or of any such complex combinations of reflex movements as certain instincts exhibit.

Finally it is this fundamental property of the affective tendency of constituting in some degree a force gravitating toward that environment or those particular environmental relations which permit the reactivation of certain mnemonic accumulations forming this very tendency, which lends that environment or those environmental relations the appearance of a *vis a fronte* or "ultimate cause" differing very essentially from the *vis a tergo* or "actual cause" which alone is operative in inorganic nature.[49]

The organism, writes Jennings, "seems to work toward a definite purpose. In other words, the final result

[49]See W. James, *Principles of Psychology,* I. pp. 7 f. London, Macmillan, 1901.

of its action seems to be present in some way at the beginning, determining what the action shall be. In this the action of living things appears to contrast with that of inorganic things." [50]

Now this "final result of its action" exists really from the beginning in the form of mnemonic accumulation. For that environment or those special environmental conditions to which the animal is gravitating operate now as *vis a fronte* in so far as they were formerly *vis a tergo* and in so far as the physiological activities then determined by them in the organism have left behind a mnemonic accumulation which now itself constitutes the real and true *vis a tergo* moving the living being.[51]

Thus it is clear that one and the same explanation applies to all the "finalism" of life. For from the ontogenetic development which creates organs that cannot perform their functions until the adult state, to the tendency of all physiological states determined by certain environmental conditions to remanifest themselves at the first appearance of phenomena usually preceding these conditions, but in no wise constituting them; from the perfect way in which the organism in its entirety is morphologically adapted to its environment before the latter can exercise its formative influence, to all the wonderful formations and special structures so exactly adapted to all the most probable conditions to which this organism might later be exposed; from the simplest reflex motions that are directed so perfectly toward the preservation and welfare of the individual to the most complex instincts by means of

[50]Jennings, *Behavior of Lower Organisms,* p. 338.

[51]E. Mach, *Die Analyse der Empfindungen,* 5th ed., pp. 79, 78, Jena, Fischer; English edition: Chicago, Open Court Publishing Company, 1897.

which animals prepare in advance for future conditions of which they themselves are probably ignorant—all these "finalistic" phenomena of life, identical in their nature, can be explained as so many manifestations of a purely mnemonic nature, as we have seen in our earlier writings mentioned above.

And now in the present essay we see that affective tendencies, which are even more conspicuously "finalistic" manifestations, are likewise based upon the mnemonic property of living substance, and hence in the last analysis upon the faculty of "specific accumulation," a faculty belonging exclusively to the nervous energy which underlies all life.

This mnemonic property, this faculty of "specific accumulation," which by its absence leaves inorganic nature exclusively in the power of forces *a tergo* and deprives it of every finalistic aspect, is on the other hand everywhere present in organic nature and because of its presence makes the world of life a world apart, of which the most characteristc elements cannot be explained by the laws of physics and chemistry alone in the limited sense assigned to them to-day.

EUGENIO RIGNANO.

MILAN, ITALY.

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